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CONTENTS

Sarah Lemer
David Combosch
Don Dumale
Filipina Sotto
Victor Soliman
Gonzalo Giribet
The family Pinnidae (Bivalvia) in the Philippine archipelago: observations on its distribution and phylogeography 137

Jeffrey H.R. Goddard
Craig Hoover
Distribution, seasonality, and prey specificity of *Flabellina goddardi* Gosliner, 2010 (Gastropoda: Nudipleura: Aeolidina) 146

Kennia Morales
Roland Sánchez
Paulina Bruning
Leyla Cárdenas
Patricio H. Manríquez
Antonio Brante
A multiple microsatellite assay to evaluate the mating behavior of the intensively exploited marine gastropod *Concholepas concholepas* (Bruguière, 1789) (Gastropoda: Muricidae) 153

Kazutaka Amano
Anton Oleinik
Aneistrolepidin gastropods (Buccinidae) from the upper Eocene hydrocarbon seep deposits in Hokkaido, northern Japan 158

G. Thomas Watters
Parachondria joyeuse: a peculiar new species of Hispaniolan Annulariidae (Gastropoda: Littorinoidea) 164

In Memoriam 166

Book Review 168

Author Index 171

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The family Pinnidae (Bivalvia) in the Philippine archipelago: observations on its distribution and phylogeography

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ABSTRACT

The Philippine archipelago, located in the northern apex of the Coral Triangle, is known for its high diversity and endemism, both caused by a complex physical setting modelled by the long tectonic history of the archipelago and by the more recent Pleistocene sea-level fluctuations. In order to assess the influences of the complex Philippines geography on benthic marine species, we conducted phylogenetic and phylogeographic analyses on 71 specimens (out 112 originally collected) of ten species of Pinnidae, sequencing two mitochondrial and two nuclear markers. Our results suggest that the Philippines is a diversity hotspot for pinnids, with all sampling sites hosting three or more species, but with marked differences in species composition in each site, indicating that most pinnids have a patchy distribution. Our data also suggest that most species exhibit high levels of genetic connectivity even over large geographical distances. As previouly suggested, our data also support the idea that the nominal taxon *Pinna atropurpurea* includes at least 2 cryptic species in the Philippines.

Additional Keywords: pen shell, cryptic species, diversity hotspot, biogeography

INTRODUCTION

The Coral Triangle is recognized as a global center of marine species biodiversity (e.g., Hughes et al., 2002; Veron et al., 2009; Carpenter et al., 2011; Bellwood et al., 2012; Briggs and Bowen, 2013), and is thus relatively well studied from a biological perspective (reviewed in Hoeksema, 2007). Within the Coral Triangle region, complex marine currents and successive sea level fluctuations are thought to have given rise to vicariant barriers promoting genetic divergence among marine populations (Briggs, 1999a; Briggs, 1999b; Mora et al., 2003). Located at the intersection of six tectonic plates, the Coral Triangle lies between the Pacific and Indian Oceans, encompassing both sides of a major marine biogeographical break known as the Sunda Shelf barrier (Lourie et al., 2005), which favors genetic divergence among populations. Finally the very diverse and extensive habitats found in the region can also be responsible for its high biodiversity by creating a refuge from extinction for various marine species (Wilson and Rosen, 1998; Bellwood and Meyer, 2009). The Philippine archipelago is located at the northern apex of the Coral Triangle, which also encompasses the Indo-Malay region, New Guinea, and the Solomon Islands (Figure 1), and is especially known for its high species diversity and endemism (Jones and Kennedy, 2008). The complex physical environment of the Philippine archipelago is a result of its old and convoluted tectonic history (Hall, 2002), recent changes in coastlines and basin boundaries associated with Pleistocene sea-level fluctuations (Sathiamurthy and Voris, 2006), and present-day oceanographic circulation patterns (e.g., seasonal currents; Han et al., 2009). As a result, this region has shown to strongly influence dispersal and isolation of marine organisms over evolutionary and ecological timescales and to shape genetic structure and species distribution (Juinio-Menez et al., 2003; Ravago-Gotanco and Juinio-Menez, 2004; Lourie, et al., 2005; Ravago-Gotanco et al., 2007; Payo et al., 2013). However, most phylogeographic studies conducted in the area focused mainly on single species and little has been done to simultaneously study multiple taxa

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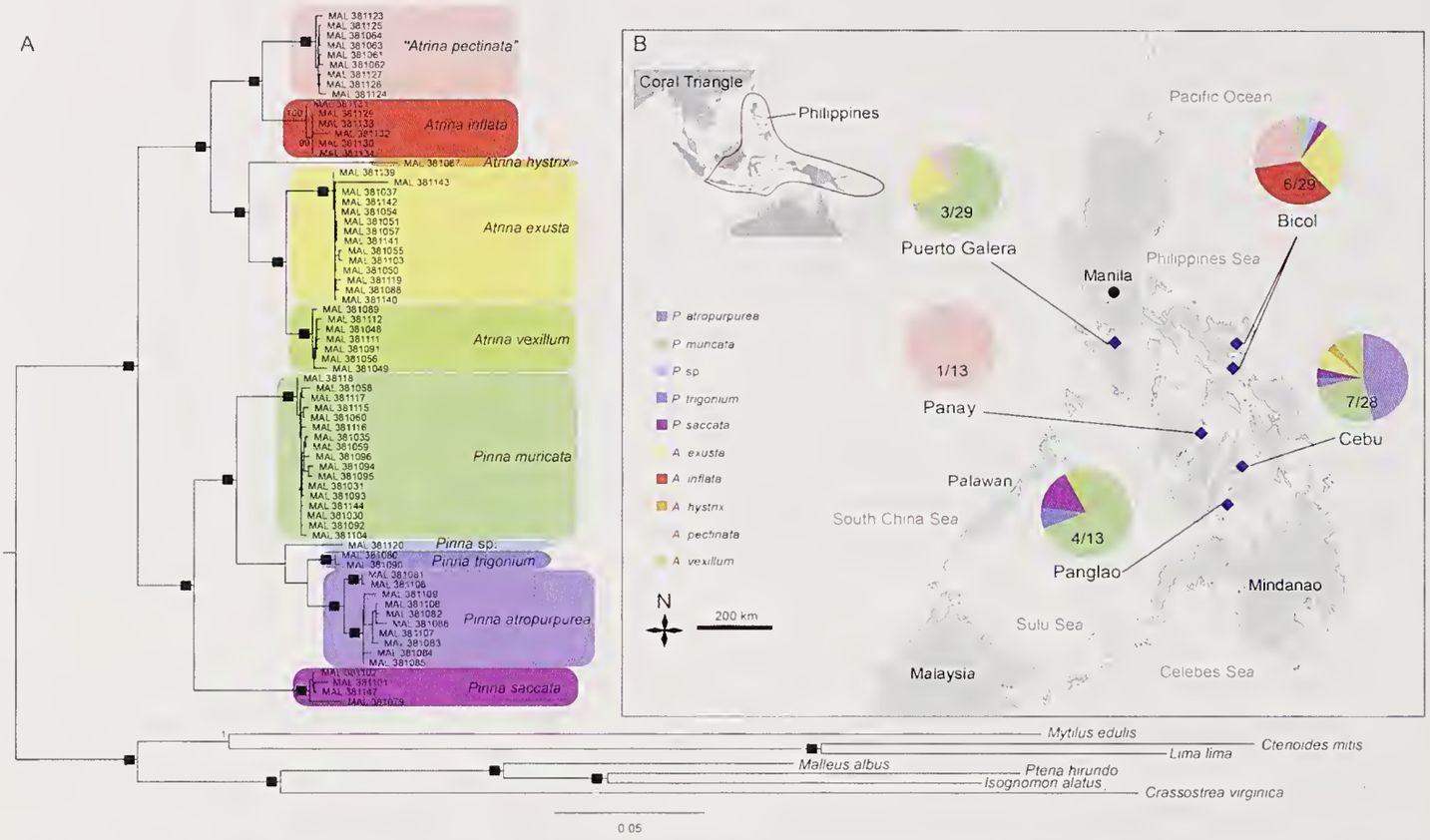

Figure 1. (A) Phylogenetic relationships of Philippine Pinnidae species inferred from the combined maximum likelihood analysis of four genetic markers (COI, 16S rRNA, 18S rRNA and 28S rRNA). Black squares represent nodes supported by both ML and Bayesian analyses (>90% bootstrap support or >1.0 posterior probability). (B) Map of sampled localities. The total number of species and of specimens per species is represented as pie charts for each locality.

or higher taxonomic levels (i.e., genera or families, but see review in Carpenter et al., 2011).

Members of the family Pinnidae are commercially important, large fan-shaped bivalves often found buried in muddy or sandy substrates of mangroves or seagrass beds, but also embedded in coral heads. Pinnids are widely distributed in temperate to tropical waters in the Indo-Pacific, Atlantic, and Mediterranean Sea. Many species are commonly found in the Philippine archipelago, where some are popular food items, e.g., *Atrina pectinata* (Linnaeus, 1767) and *Atrina inflata* (Dillwyn, 1817). Pinnids have a considerable amount of meat (mostly the adductor muscle) and their extraction is not regulated in the Philippines, causing them to become a target economic species that can potentially be overfished. The family contains two currently recognized genera and 55 accepted species (Turner and Rosewater, 1958; Rosewater, 1961; Schultz and Huber, 2013; Lemer et al., 2014). At least 15 species are found in the archipelago (Poppe, 2010; Schultz and Huber, 2013), which renders the Philippines the region with the highest known pinnid diversity in the world. A recent phylogenetic analysis based on four genetic markers (Lemer, et al., 2014) identified cryptic species in several morphospecies known to display a wide Indo-Pacific distribution, including *Pinna muricata* Linnaeus, 1758; *P. saccata* Linnaeus, 1758, *P. atropurpurea* G.B. Sowerby I, 1825, *Atrina assimilis* (Reeve, 1858), *A. exusta* (Gmelin, 1791), and *A. pectinata* (Linnaeus, 1767). However, no study has focused on the Philippine pinnid diversity using genetic markers, despite the fact that the region may host multiple cryptic species.

Within this context, the major goal of this study is to provide insights into the pinnid species diversity in the Philippine archipelago and to compare evolutionary and life history strategies among species.

MATERIALS AND METHODS

Specimens were collected by SL and DC during a field trip to the Philippines in May 2013. A total of 112 specimens from ten morphospecies were sampled by snorkelling and SCUBA diving or obtained from fishermen (samples from Panay) in 5 sites in the vicinities of Puerto Galera (Mindoro), Panay, Cebu, Panglao (Bohol) and Bicol (Tables 1, 2; Figure 1). For each locality, we surveyed both a sandy bay and a coral reef area to optimize habitat and species diversity. In total, three localities were surveyed in the Cebu region, four in Puerto Galera, two in Panglao and three in Bicol (Table 2). Due to difficult sea conditions, only 18 specimens were obtained from fishermen at two localities in Panay.

The 112 specimens reported in Table 1 were used to describe species composition at each site. Molecular

Table 1. Number of specimens of each species sampled per study site.

Sites	*P. atropurpurea*	*P. nuricata*	*Pinna* sp.	*P. trigonium*	*P. saccata*	*A. exusta*	*A. inflata*	*A. hystrix*	*A. pectinata*	*A. vexillum*	Total per site
Bicol	0	1	1	0	1	8	10	0	8	0	**29**
Panglao	0	9	0	1	2	0	0	0	0	1	**13**
Cebu	13	7	0	1	1	2	0	1	0	3	**28**
Panay	0	0	0	0	0	0	0	0	13	0	**13**
Puerto Galera	0	20	0	0	0	6	0	0	0	3	**29**
Total per species	13	37	1	2	4	16	10	1	21	7	112

analyses were conducted on 71 samples out of the 112 specimens (Table 2), due to export permit difficulties with specimens from some locations. The 71 specimens used for genetic analyses are deposited in the Malacology collection of the Museum of Comparative Zoology, with relevant data accessible through MCZbase (mczbase.mcz.harvard.edu; Table 2). Molecular markers consisted of two nuclear ribosomal genes: the nearly complete 18S rRNA (1.7 Kb) and a ca. 2 Kb fragment of 28S rRNA; and two mitochondrial fragments for 16S rRNA (510 bp) and cytochrome *c* oxidase subunit I (650 bp; hereafter COI). DNA extraction, amplification, sequencing, primers, and protocols are as detailed in Lemer et al. (2014). Sequence data were visualized and edited in Geneious Pro 5.3.4 (Drummond et al., 2010) and aligned with muscle (Edgar, 2004) as implemented in Geneious. All new sequences have been deposited in GenBank and all new and previously analyzed sequences (Lemer et al. 2014) are listed in Table 2. Outgroup sequences were obtained from Bieler et al. (2014).

Maximum likelihood (ML) analyses were conducted using RAxML v. 7.2.7 (Stamatakis, 2006) on the four concatenated genes—the goal of these analyses being to test the membership of individual specimens to a particular species, and not for reconstructing the phylogeny of the familiy Pinnidae, since this has already been done elsewhere (Lemer et al. 2014). For the ML searches, a General Time Reversible model with a discrete gamma distribution of site-rate heterogeneity (GTR + Γ) was specified for each individual data partition (i.e., gene). Nodal support was estimated via 1000 replicates of a rapid bootstrap algorithm (Stamatakis et al., 2008) using the GTR-GAMMA model, via the Cyberinfrastructure for Phylogenetic Research (CIPRES) portal (Miller et al., 2010). Bootstrap resampling frequencies were thereafter mapped onto the optimal tree from the independent searches.

Bayesian phylogenetic analyses were conducted in Beast v1.61 (Drummond and Rambaut, 2007) on the four concatenated genes, under the GTR+ Γ substitution model for each of 18S rRNA, 16S rRNA and COI and under the HKY + Γ model for 28S rRNA, as recommended by *j*ModelTest 2 (Darriba et al., 2012). COI sequences were partitioned into two sets by codon positions, separating third positions from the set of first and second positions. A relaxed uncorrelated lognormal clock model was inferred for each partition. The Yule speciation model was assumed for the tree prior and the starting tree was randomly generated. Markov chains were run for 10,000,000 generations, sampling every 1000th generation, until convergence. Convergence diagnostics were assessed using TRACER v1.5 (Rambaut and Drummond, 2007). Five independent runs were subsequently conducted and combined using LogCombiner (http://beast.bio.ed.ac.uk/LogCombiner). Phylogenetic trees were summarized as maximum clade credibility trees (MCCT), with branch lengths in substitutions per site after a burn-in of 10,000 in Tree Annotator v.1.6.2. in the Beast package (http://tree.bio.ed.ac.uk/software/tracer).

Table 2. List of samples included in the genetic analyses. Total number of specimens per species is given as well as the number of specimens per locality, MCZ Malacology voucher numbers, sampling sites, GPS coordinates, and GenBank accession numbers for each.

Species	*n*	MZC Accessions	Sampling site	GPS coordinates	COI	16S rRNA	18S rRNA	28S rRNA
Pinna atropurpurea	6	MAL 381081 - 381086	Caubian Reef (Cebu Island)	10°16′53.93″ N / 124°11′02.69″ E	KU987199 - KU987201	KJ365564 - KJ365566	KJ365801 - KJ365803	KJ366080 - KJ366082
Total $n = 10$	4	MAL 381106 - 381109						
Pinna muricata	3	MAL 381030, 381031, 381035	Back Beaeh (Puerto Galera)	13°30′29.65″ N / 120°56′44.51″ E	KJ366475	KJ365709	KJ365975	KJ366259
Total $n = 17$	3	MAL 381058 - 381060	Mindolo Bay (Puerto Galera)	13°30′25.69″ N / 120°54′58.21″ E	KJ366481	KJ365715	KJ365981	KJ366265
	5	MAL 381092 - 381096	Panglao Island (Bohol Island)	9°33′36.38″ N / 123°44′05.49″ E	KJ366324	KJ365525	KJ365752	KJ366031
	1	MAL 381104	Caubian Reef (Cebu Island)	10°16′53.93″ N / 124°11′02.69″ E	KU987212	KU987062	KU987112	KU987163
	4	MAL 381115 - 381118	Mactan Island (Cebu Island)	10°17′03.46″ N / 124°00′06.06″ E	KU987202, KJ366371	KJ365568, KJ365569	KJ365805, KJ365806	KJ366084, KJ366085
	1	MAL 381144	San Miguel Island (Bicol)	13°22′50.21″ N / 123°49′26.26″ E	KU987213	KU987063	KU987113	KU987164
Pinna sp.	1	MAL 381120	Tabaco City Cove (Bicol)	13°22′17.89″ N / 123°44′09.62″ E	KU987214	KU987064	KU987114	KU987165
Total $n = 1$								
Pinna trigonium	2	MAL 381080	Caubian Reef (Cebu Island)	10°16′53.93″ N / 124°11′02.69″ E	-	KJ365563	KJ365800	KJ366079
Total $n = 2$		MAL 381090	Panglao Island (Bohol Island)	9°33′36.38″ N / 123°44′05.49″ E	-	KU987065	KU987115	KU987166
Pinna saccata	1	MAL 381079	Olango Island (Cebu Island)	10°17′26.27″ N / 124°04′40.74″ E	KJ366370	KJ365567	KJ365804	KJ366083
Total $n = 4$	2	MAL 381101, 381102	Panglao Island (Bohol Island)	9°32′31.69″ N / 123°42′31.48″ E	-	KU987066	KU987116, KU987117	KU987167, KU987168
	1	MAL 381147	San Miguel Island (Bicol)	13°22′59.71″ N / 123°49′50.65″ E	-	KU987067	KU987118	KU987167, KU987168
Atrina exusta	1	MAL 381037	Back Beach (Puerto Galera)	13°30′29.65″ N / 120°56′44.51″ E	KJ366476	KJ365710	KJ365976	KJ366260
Total $n = 14$	2	MAL 381050, 381051	Mindolo Bay (Puerto Galera)	13°30′25.69″ N / 120°54′58.21″ E	KJ366478, KU987216	KJ365712, KU987069	KJ365978, KU987120	KJ366262, KU987171
	2	MAL 381054, 381055	Pirate Cove (Puerto Galera)	13°30′27.65″ N / 120°57′48.53″ E	KJ366479, KU987217	KJ365713, KU987070	KJ365979, KU987120	KJ366263, KU987172
	1	MAL 381057	Matabang Parang (Puerto Galera)	13°30′47.72″ N / 120°57′47.08″ E	KU987215	KU987068	KU987119	KU987170
	1	MAL 381088	Caubian Reef (Cebu Island)	10°16′53.93″ N / 124°11′02.69″ E	KU987218	KU987071	KU987122	KU98717

(*Continued*)

Table 2. (Continued)

Species	*n*	MZC Accessions	Sampling site	GPS coordinates	COI	16S rRNA	18S rRNA	28S rRNA
	1	MAL 381103	Mactan Island (Cebu Island)	10°19′27.10″ N / 124°01′35.77″ E	KU987219	KU987072	KU987123	KU987174
	1	MAL 381119	Tabaco City Cove (Bicol)	13°22′17.89″ N / 123°44′09.62″ E	KU987220	KU987073	KU987124	KU987175
	5	MAL 381139 - 381143	San Miguel Island (Bicol)	13°22′50.21″ N / 123°49′26.26″ E	KU987221 - KU987225	KU987074 - KU987078	KU987125 - KU987129	KU987176 - KU987180
Atrina inflata	6	MAL 381129 - 381134	Sorsogon Bay (Bicol)	12°57′58.31″ N / 124°00′15.26″ E	KJ366322, KU987226 - KU987230	KJ365523, KU987079 - KU987083	KJ36575, KU987130 - KU987134	KJ366029, KU987181 - KU987185
Total $n = 6$								
Atrina lystrix	1	MAL 381087	Caubian Reef (Cebu Island)	10°16′53.93″ N / 124°11′02.69″ E	KJ366369	KJ365562	KJ365799	KJ366078
Total $n = 1$								
Atrina pectinata	4	MAL 381061 - 381064	Ajuy (Panay Island)	11°09′39.55″ N / 123°01′43.13″ E	KU987231 - KU987234	KU987084 - KU987086	KU987135 - KU987138	KU987186 - KU987189
Total $n = 9$	5	MAL 381123 - 381127	Sorsogon Bay (Bicol)	12°56′19.25″ N / 124°00′07.56″ E	KU987235 - KU987239	KU987087 - KU987091	KU987139 - KU987143	KU987190 - KU987194
Atrina vexillum	2	MAL 381048, 381049	Mindolo Bay (Puerto Galera)	13°30′25.69″ N / 120°54′58.21″ E	KJ366477, KU987240	KJ365711, KU987092	KJ365977, KU987144	KJ366261, KU987195
Total $n = 7$	1	MAL 381056	Matabang Parang (Puerto Galera)	13°30′47.72″ N / 120°57′47.08″ E	KJ366480	KJ365714	KU987096	KJ366264
	2	MAL 381089, 381112	Mactan Island (Cebu Island)	10°17′09.65″ N / 124°00′02.11″ E	KU987241, KU987242	KU987093, KU987095	KU987145, KU987146	KU987196, KU987191
	1	MAL 381111	Caubian Reef (Cebu Island)	10°16′53.93″ N / 124°11′02.69″ E	KU987243	KU987094	KU987147	KU987198
	1	MAL 381091	Panglao Island (Bohol Island)	9°33′36.38″ N / 123°44′05.49″ E	KJ366323	KJ365524	KJ365751	KJ366030
Total *n* samples	71							
Outgroups								
Isognomon alatus	1	BivAToL-30	Florida, USA		KC429251	KC429096	KC429333	KC429426
Pteria hirundo	1	BivAToL-126	Spain		KC429250	AF120647	KC429332	KC429425
Malleus albus	1	BivAToL-79	Australia		KC429252	KC429097	KC429334	KC429427
Mytilus edulis	1	BivAToL-271	U.K.		KC429249	KC429095	KC429331	KC429424
Lima lima	1	BivAToL-114	Spain		KC429257	KC429101	KC429339	KC429434
Ctenoides mitis	1	BivAtoL-28	Florida, USA		KC429150	-	KT75792	KT757839
Crassostrea virginica	1	BivAToL-276	Florida, USA		KC429253	KC429098	KC429335	KC429429

Sequences of COI and 16S rRNA were collapsed into haplotypes using DnaSP and treated as alleles for the subsequent intra-species analyses. The genealogical relationships among haplotypes for each species with 4 or more haplotypes per marker were assessed by constructing haplotype networks using a median joining algorithm as implemented in the software NETWORK 4.6.1.1 (http://www.fluxus-engineering.com). A parsimony algorithm was subsequently applied to represent the most parsimonious intraspecific phylogenies (Polzin and Daneshmand, 2003).

RESULTS AND DISCUSSION

Although Pinnidae is a relatively diverse family, encompassing about 55 accepted species found in all of the world's warm oceans, local species diversity is usually low (Rosewater, 1961). The majority of pinnid species inhabit sandy bottoms or mudflats in shallow waters, mangroves or coral reefs (although some deeper species exist; Rosewater, 1961; Schultz and Huber, 2013). However, more than one species rarely occur in the same site. This contrasts with the Philippines, where in four sampled regions (Puerto Galera, Cebu, Panglao and Bicol) at least three different species of pinnids coexist. Although most sites have a comparable number of species, species composition varies among sites (based on the 112 specimens reported in Table 1), indicating that pinnid species tend to have patchy distributions. This was corroborated by our field observations, which revealed that most species are represented by small clusters of individuals. A common pattern was found for *Pinna muricata*, *P. atropurpurea*, *Atrina pectinata*, and *A. inflata*; when these species were present at a site, they were usually the most abundant, with only a few representatives of one or more additional species found among them. For example, our sampled site in the Cebu region was dominated by *P. atropurpurea* (12 specimens) and *P. muricata* (7 specimens), complemented by a few specimens of other species (1 specimen of *P. trigonium*, 1 of *A. hystrix*, 2 of *A. exusta*, 3 of *A. vexillum*, and 1 of *P. saccata*; Table 1). Similarly, the Bicol region was dominated by *A. inflata*, *A. pectinata*, and *A. exusta* (10, 8, and 8 specimens, respectively) with only a few representatives of other species (1 specimen of *Pinna* sp., 1 of *P. muricata*, and 1 of *P. saccata*). A similar pattern of species distribution has been previously observed in a study assessing the biodiversity and distribution of Pinnidae in Malaysia (Idris et al., 2008) and might indicate inter-species competition for habitat and resources in each site and/or different reproductive strategies (e.g., low larval recruitment). A broader sampling in the Philippines would allow confirming this hypothesis by estimating species richness, evenness, and diversity indices.

The ML analyses of the four concatenated genes ($-\ln L$=28,492.9666) and the Bayesian analysis produced nearly identical trees (Figure 1). As previously observed by Lemer et al. (2014), *Atrina* and *Pinna* are reciprocally monophyletic. Within each genus, the relationships among species match previous findings based on molecular data including additional species (Lemer et al., 2014), with *A. inflata* being the sister species to a group identified as "*A. pectinata*" (although *A. pectinata* has recently been attributed to the Indian Ocean only (Schultz and Huber, 2013). *Atrina hystrix* (Hanley, 1858) is the sister species to a clade composed of *A. exusta* and *A. vexillum*. *Pinna muricata* appears as the sister species to a clade composed of *Pinna* sp., *P. trigonium* and *P. atropurpurea*. *Pinna saccata* is the most basal clade within the represented *Pinna*, appearing as sister group to all other represented species—but it nests within *Pinna* in more comprehensive pinnid phylogenies (Lemer et al., 2014). All nodes are well supported with bootstrap support values >90% and posterior probability (pp) values of 1.00. Both the ML and Bayesian trees show a deep split between two main subclades within *P. atropurpurea* (Figure 1). Most haplotype networks obtained for each analyzed species, except for *P. atropurpurea*, display a star-like pattern with one main central haplotype shared by multiple localities, and numerous unique haplotypes separated by one or two mutational steps (Figure 2). This pattern, commonly found in populations that have undergone a recent demographic expansion, is not as clear for *A. inflata* due to the small sample size, and is absent in the well-sampled *P. atropurpurea*, which may constitute more than one species (see Lemer et al., 2014).

None of the networks obtained display clear geographical structure among the sampled sites. On the contrary, in several instances distant localities shared identical haplotypes (Figure 2; observed for *P. muricata*, *A. pectinata*, *A. exusta* and *A. vexillum*). This result tends to indicate that despite the complex and fragmented basins of the Philippines, Pinnidae species show high levels of genetic connectivity. Habitat fragmentation usually tends to limit dispersal capacity and thus lowers connectivity among populations, even for broadcast-spawning bivalves with long pelagic larval duration (PLD) (Benzie et al., 2002; Kenchington et al., 2006; Lind et al., 2007a; Lind et al., 2007b). However, low or absent genetic structure has been previously observed in other pteriomorphian bivalves with a long PLD inhabiting fragmented habitats. For example, in a study conducted with hypervariable microsatellite loci, the black-lipped pearl oyster *Pinctada margaritifera* showed little indication of genetic structure across French Polynesia (Lemer and Planes, 2014). Very little is known about the reproductive strategies and the pelagic larval duration of most pinnid species, with some exceptions for commercially important species. Most species are believed to be gonochoristic, to reproduce annually and to produce larvae with a long planktotrophic phase with trochophore and veliger stages, such as *Pinna atropurpurea*, *Atrina pectinata*, and *Atrina maura* (Sowerby I, 1835) (Beer and Southgate, 2006; Mendo et al., 2011). The potentially long PLD of pinnid species could thus enable the observed high dispersal capacity,

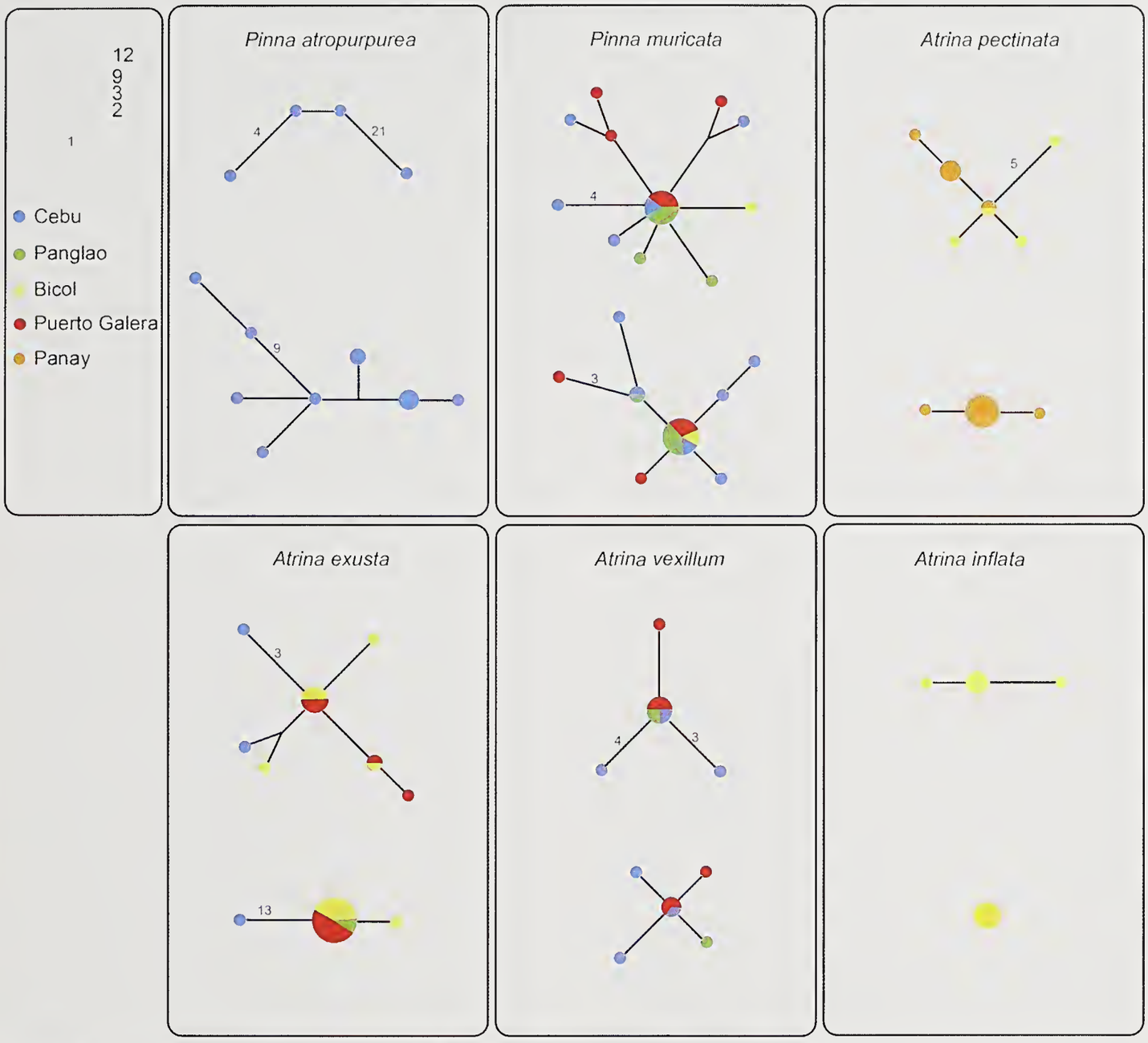

Figure 2. Haplotype networks for species with four or more samples, using COI (above) and 16S rRNA (below). Lines between haplotypes are proportional to the number of mutational steps, unless indicated by a number.

even in the highly fragmented habitat context of the Philippine archipelago.

The haplotype networks obtained for *P. atropurpurea* for COI and 16S rRNA show unique haplotypes separated by up to 21 mutational steps. Both the phylogenetic and the non star-like haplotype networks observed for *P. atropurpurea* support our previous conclusion: *P. atropurpurea* is non-monophyletic in the Pacific Ocean (Lemer et al., 2014). In addition, at least two cryptic species exist in the Philippines. Further work should thus be conducted to unravel the complexity of this taxon. In fact, *P. atropurpurea* appears to be an intricate species complex composed of cryptic species. Since Rosewater's (1961) taxonomical revision, *P. atropurpurea*, which was initially described with a distribution limited to the Central Pacific Ocean (Indonesia, Japan, and the Philippines; Winckworth, 1929), was lumped with *P. bicolor* (from the Red Sea), *P. dolabrata* Lamarck, 1819 (from Southwest Australia), *P. menkei* Reeve, 1858, and *P. madida* Reeve, 1858 (from Northeast Australia) into a single species with a wide Indo-Pacific distribution, under the name *P. bicolor*. Recent morphological (Schultz and Huber, 2013) and molecular (Lemer, et al., 2014) work reattributed or supported the original name for each of the former species in each region of the Indo-Pacific.

To conclude, in this study we aimed at assessing the species and genetic diversity of the commercially

important family Pinnidae in the Philippine archipelago, where pinnids reach their known peak of diversity. For this purpose we obtained 112 specimens, representing 10 of the 15 species known to be present in the region, from which 71 were genotyped. Our results suggest that the Philippines is indeed a diversity hotspot for the family with all sampled sites hosting three or more species but with marked differences in species composition in each site (Table 1). As previously suggested by Lemer et al. (2014), it appears that *Pinna atropurpurea* is a non-monophyetic species including at least 2 cryptic species in the Philippines.

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Distribution, seasonality, and prey specificity of *Flabellina goddardi* Gosliner, 2010 (Gastropoda: Nudipleura: Aeolidina)

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ABSTRACT

The aeolid nudibranch sea slug *Flabellina goddardi* Gosliner, 2010 was described from a single specimen found intertidally at Tarpits Reef, Carpinteria, California, in 2008. Recently, it has also been found subtidally at Anacapa Island and two sites off Malibu, California. We sampled for this species at the type locality intermittently from November 2008 to June 2016 and here report on its seasonality, microhabitat, and diet. We found 38 total individuals of the aeolid, all from April to July, with the highest number found in May and June. Most specimens were observed underneath small ledges, on a tangled faunal mat consisting mainly of arborescent bryozoans and hydroids. Laboratory feeding trials and examination of nematocysts in the aeolid cnidosac indicated that *F. goddardi* was preying on a *Bougainvillia*-like, filiferan anthomedusan hydroid. Unlike the type specimen, many individuals of *F. goddardi* found since 2008, including subtidal specimens, possessed three white lines on the body and superficially resembled *Flabellina trilineata* (O'Donoghue, 1921), with which *F. goddardi* may form a mimicry complex. *Flabellina goddardi* is known only from the northern half of the Southern California Bight, a geographic distribution unique among Northeastern Pacific nudibranchs.

Additional Keywords: Aeolid, nudibranch, gastropod, geographic distribution, northeastern Pacific Ocean, Southern California Bight, seasonality, diet, hydroid, intertidal, subtidal, mimicry

INTRODUCTION

The aeolid nudibranch *Flabellina goddardi* Gosliner, 2010 was described based on a single specimen collected in May 2008 from Tarpits Reef (34.3869,–119.5166) in Carpinteria, California (Figure 1). The type specimen was found crawling on macroalage in a low intertidal pool, providing few clues to its prey and preferred microhabitat, but did lay an egg mass in captivity, allowing for observations of its embryonic development and hatching planktotrophic larvae (Gosliner, 2010; Goddard and Green, 2013). During sampling trips, since 2008, we have observed additional specimens of *F. goddardi* at the type locality, and in April 2014 the junior author observed the first specimen found outside the type locality, at 9 m depth in Las Flores Canyon, off Malibu, California (Goddard and Hoover, 2014) (Figure 1). More recently, additional specimens have been observed subtidally at 18 m depth on the south side of West Anacapa Island, California (Klug, 2016a, b; D. Klug, personal communication to JG, 12 May 2016) and at 9 m depth off Point Dume, Malibu (Hoover 2016) (Figure 1). Here, we describe the seasonality and microhabitat of *F. goddardi*, present evidence that it preys on a filiferan anthomedusan (athecate) hydroid, and based on our examination of the above specimens, supplement the original description of the color pattern of this delicate and distinctive species. We also discuss a potential mimicry complex involving *F. goddardi*.

STUDY SITE AND METHODS

Tarpits Reef is a sedimentary bench cut by shallow channels, pocketed with scattered pools, and short undercut ledges (Figure 2; and see images in Goddard and Hoover, 2014). The bench extends from the low intertidal into the shallow subtidal and has an intertidal area of approximately 2800 m^2. Landward it is backed by a sandy beach approximately 65 m wide and behind that a marine terrace 2 m high fronted by sandstone rip-rap and natural outcrops of asphalt (giving the reef its name). Sand levels on the beach build through the summer and can partially fill in low spots on the reef, but then decline in winter, exposing underlying bedrock and cobble.

To assess the seasonality of *F. goddardi* we searched tidepools and the undersides of ledges on Tarpits Reef, counting all individuals we found during 29 total monthly trips made from November 2008 to June 2016. After finding numerous specimens under three small ledges (e.g., Figure 2) near the landward edge of the reef in May 2011, we included those ledges in all subsequent sampling. Combining the samples by month across all years we conducted at least one search in each calendar month.

Most flabellinids feed on Hydrozoa (Thompson 1976; McDonald and Nybakken 1997), so we focused on

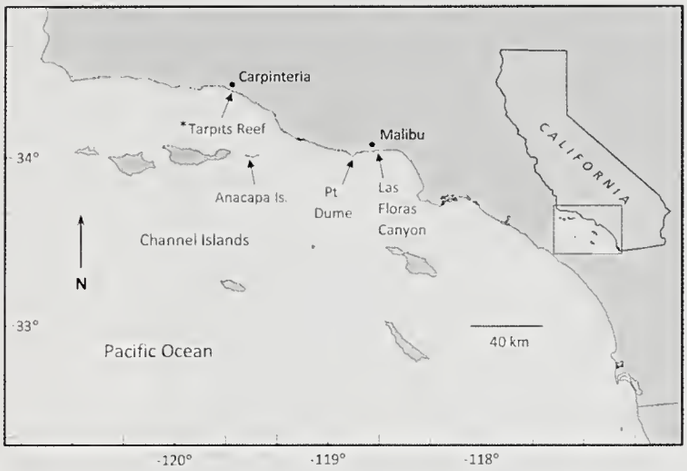


Figure 1. Map of Southern California Bight, with small arrows indicating localities where *Flabellina goddardi* has been found. Type locality indicated by asterisk (*).

members of this taxon in determining the prey of *F. goddardi*. We collected small samples of the organisms underlying the slugs at Tarpits Reef and isolated the different species of hydroids found using a dissection microscope. In a round of preliminary behavioral trials conducted in May and June 2011, we cut individual polyps from the four filiferan hydroids observed, and holding a polyp by its stalk with watch-maker's forceps, tested the reaction of individual slugs to contact on the anterior part of the head and cephalic tentacles by the polyps of each of these species. In these trials we noted the reaction of the slugs as repelled (slug quickly turned away following contact with a polyp), neutral (no obvious reaction), or attracted and tried to consume. In four feeding trials conducted separately in May 2011, June 2011, June 2012, and April 2015, we held 1–4 slugs in 250 ml glass dishes with fresh seawater for up to four days. Small pieces of each of the filiferan hydroids we

Figure 2. Rock ledge at Tarpits Reef, Carpinteria where many *Flabellina goddardi* (top inset) have been found. Lower inset shows two *F. goddardi* (inside red ovals) stranded at low tide on mixed hydrozoan and bryozoan biota underneath the ledge.

had found were placed with the slugs and checked twice daily to see which species the slugs associated with and, as judged by missing polyps and (or) coenosarc, appeared to have preyed upon. During these trials we changed the seawater in the dishes daily and kept the fragments of the different species of hydroids separated from each other. Finally, we compared the cnidome of the hydroid consumed by the slugs in the feeding trials with the nematocysts in the cnidosacs of two of the slugs. We did this by making squashes of fresh individual polyps and individual cnidosacs on microscope slides, and comparing the types and size of the component nematocysts using a compound microscope with a calibrated ocular micrometer. Four specimens of *F. goddardi* collected in May 2011 and one in June 2012 were used in some of the above trials and were deposited in the Invertebrate Zoology Collection at the California Academy of Sciences (CASIZ 186806, 186807, 195985).

RESULTS

Seasonality: Including the type specimen, we have found a total of 39 specimens of *F. goddardi* at Tarpits Reef, mainly during the spring (Figure 3). Specimens were found from April to July, with the highest total number of individuals by month observed in May and June (28 and 7 individuals, respectively). The highest number of individuals found per sampling trip was 12 in May 2011, followed by 11 in May 2014. However, no specimens were found in May 2012 and May 2013, and no specimens were found from August to March in any of the years sampled. Subtidally, *Flabellina goddardi* has been found off Malibu in May (Goddard and Hoover, 2014; Hoover, 2016) and at Anacapa Island in April and May (Klug 2016a, b). One specimen of *F. goddardi*, until recently identified as *F. trilineata* (see Discussion), was found at Anacapa Island in January 2006 (Segal 2011), indicating the presence of adults subtidally during at least some winters. Egg-laying has been observed in the field and lab in April and May.

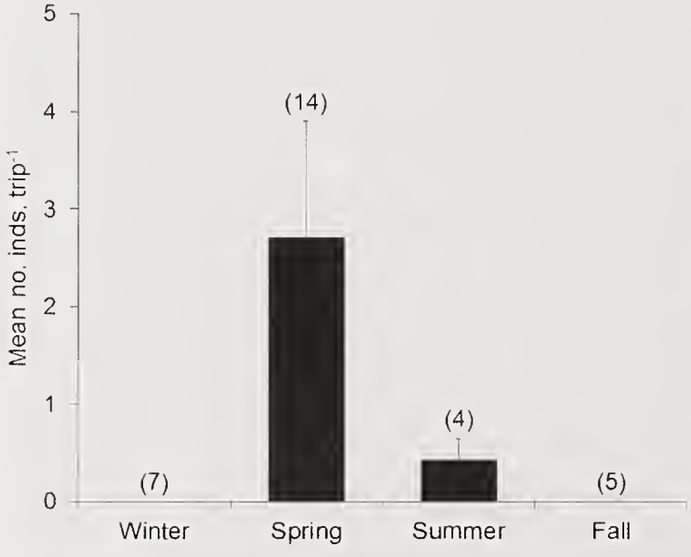


Figure 3. Seasonality of occurrence of *Flabellina goddardi* at Tarpits Reef. Data collected November 2008 to June 2016 combined by season, across all years, and also include the finding of the type specimen in May 2008 for an overall total of 30 sampling trips. Bars indicate mean (+ 1 SE) number of individuals found per monthly sampling trip, with total number of trips per season shown in parentheses. Winter = January – March, Spring = April – June, Summer = July – September, Fall = October – December.

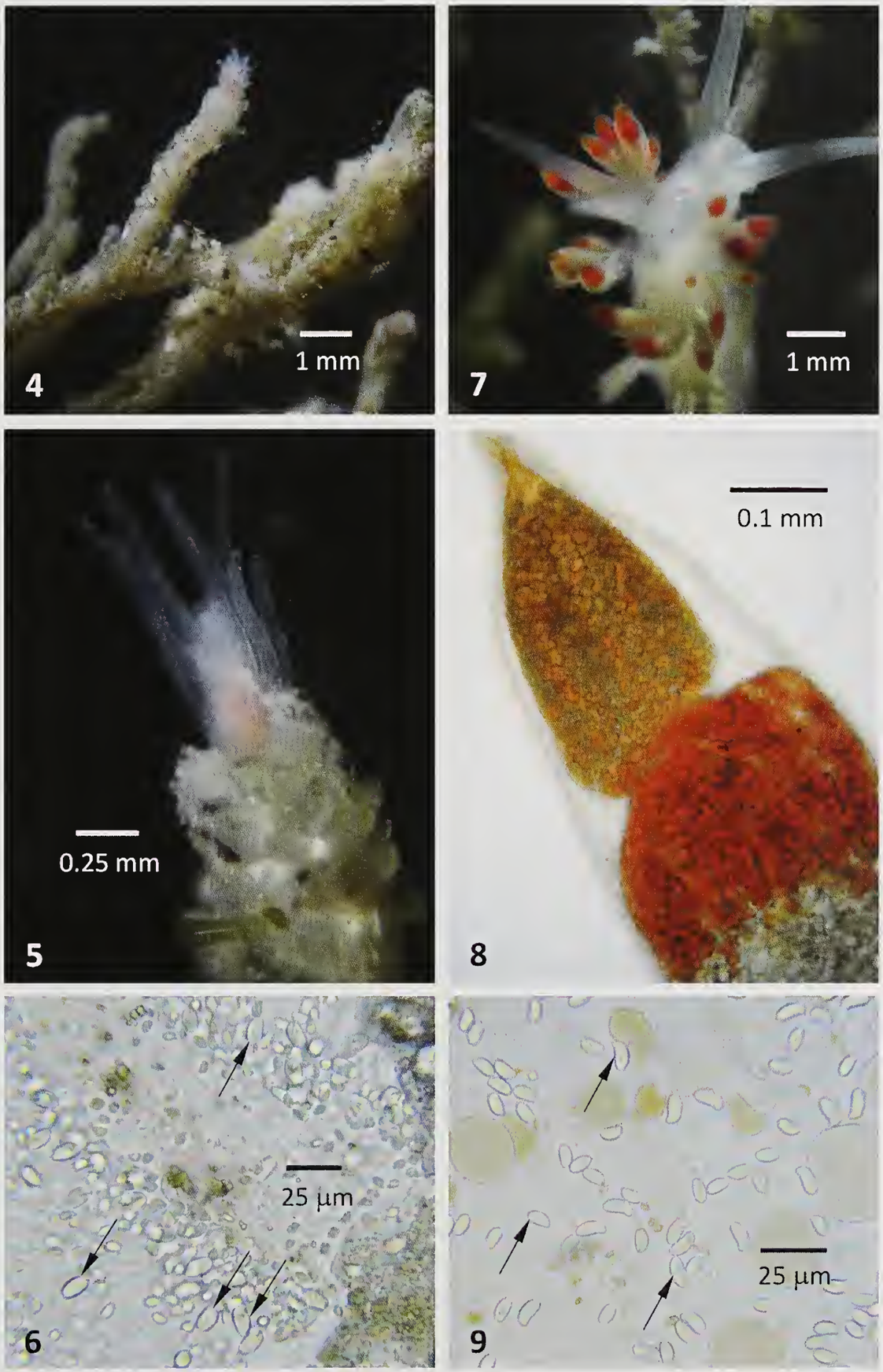
Microhabitat and Prey Specificity: All specimens of *F. goddardi* found at Tarpits Reef since discovery of the type specimen were found underneath overhanging ledges (Figure 2) on a tangled mat consisting of erect bryozoans and hydrozoans, as well as a tubular calcareous sponge, the stoloniferous octocoral *Clavularia* sp., and the slender, sand-encrusted social ascidian *Euherdmania claviformis* (Ritter, 1903) (Figure 2, lower inset). When exposed at low tide, *F. goddardi* appeared as small, but distinct semi-translucent white and red blobs on the surface of this mat (Figure 2, lower inset).

Seven species of hydrozoans were isolated out of the substrate found under *F. goddardi*. These included two leptothecate species: *Halecium* sp. and the diminutive, epibiotic *Calycella syringa* (Linnaeus, 1767), and five species of filiferan Anthoathecata. The latter included *Eudendrium* sp., *Bougainvillia*-like species A and B (both with a detritus and particle-encrusted perisarc), one *Cordylophora*-like species, and one unidentified species. *Bougainvillia*-like species B was the least abundant of the filiferan hydroids, and we did not observe it until June 2012.

In the behavioral trials, *F. goddardi* was repelled by contact near the mouth with individual polyps of *Eudendrium* sp., the *Cordylophora*-like species, and the unidentified filiferan hydroid, and showed no obvious reaction to *Bougainvillia*-like species A (as mentioned above, we had not found *Bougainvillia*-like species B when these trials were conducted).

In the feeding trials, *F. goddardi* crawled onto and remained and fed only on *Bougainvillia*-like species B (Figures 4, 5, 7), which after three days had lost its polyps and a significant amount of coenosarc. Additionally, one specimen of *Flabellina goddardi* which was isolated with this species for three days and then held without food for an additional six days grew from 8.5 mm to 12.5 mm (total crawling length measured with digital calipers) and also regenerated a cluster of posterior cerata that had been missing at the time of collection.

Comparison of the cnidome of *Bougainvillia*-like species B with *F. goddardi* cnidosacs (Figure 8) revealed matching microbasic euryteles (Figures 6, 9). In addition, the hydroid polyps (Figure 5) contained smaller desmonemes (Figure 6). The microbasic euryteles from one cnidosac of a *F. goddardi* that had been feeding on *Bougainvillia*-like species B for 48 hours averaged



Figures 4–9. Hydrozoan prey of *Flabellina goddardi*. **4.** *Bougainvillia*-like species B. **5.** Polyp of *Bougainvillia*-like species B. **6.** Photomicrograph of squash of polyp of *Bougainvillia*-like species B with arrows indicating microbasic euryteles. **7.** *Flabellina goddardi* on *Bougainvillia*-like species B. **8.** Tip of a ceras of *F. goddardi*, showing cnidosac and subapical red-orange band. **9.** Photomicrograph of squash of ceras tip of *F. goddardi*, with arrows indicating microbasic euryteles.

10.7 µm long (SD = 1.9 µm, n = 16), not significantly different from those from one polyp of its prey, which averaged 11.9 µm long (SD = 2.0 µm, n = 11) (2 tailed t-test assuming equal variances, p = 0.13, MS Excel 2013).

We did not observe gonophores or other reproductive structures on *Bougainvillia*-like species B. Therefore, although it resembles *Bougainvillia muscus* illustrated in fig. 40A of Marques et al. (2007), it could be in other genera of the Bougainvilliidae, or even the Pandeidae, all of which have cnidomes consisting of microbasic euryteles and desmonemes (P. Schuchert, personal communication to JG, 20 April 2015). The tentacles of *Bougainvillia*-like species B lacked pigment, but the hypostomes were salmon-colored. The coenosarc of the hydroid was obscured by the particle-encrusted perisarc, but did not appear to have much pigmentation (Figures 4, 5).

Color Pattern: All specimens of *F. goddardi* found to date have cerata with bright orange cnidosacs, a subapical red band, and milky to pale olive digestive diverticula (Figures 2, upper inset; 7, 8). In the specimens from Anacapa Island, the subapical red band blends into bright orange which extends half way or more down each ceras (Figure 10). The body, head, cephalic tentacles, rhinophores, and tail are all translucent white. While the type specimen of *F. goddardi* lacked encrusting white pigment (Gosliner, 2010), many specimens found since 2008 have possessed broken to relatively complete, encrusting white lines, one dorsal and medial, running from the tail to the head, where it bifurcates and continues dorsally along each cephalic tentacle, and one along each side of the body, just below the cerata, which converge at the tail (Figure 10; Goddard and Hoover, 2014). In some specimens these white lines were incomplete (e.g., see https://www.flickr.com/photos/34486353@N07/5744824564), or were represented by mere traces and fragments. Additionally, some of the subtidal specimens had a white line running up the posterior side of each rhinophores (e.g., Figure 10).

Figures 10–13. *Flabellina goddardi* and other nudibranchs with similar color patterns found at Anacapa Island, California, spring 2016. **10.** *Flabellina goddardi*. **11.** *Flabellina trilineata*. **12.** southern form of *Limacia cockerelli*. **13.** *Austraeolis stearnsi*. All images by Douglas Klug.

DISCUSSION

In the eight years since its discovery, *F. goddardi* has been observed at a single intertidal locality and three subtidal localities, all in the northern half of the Southern California Bight (SCB) (Figure 1), which is at the southern extent of the California Transition Zone, part of the Oregon Biogeographic Province (Briggs and Bowen, 2012). A few other Northeastern Pacific nudibranchs appear to have even more restricted geographic distributions (e.g., *Cuthona hamanni* Behrens, 1987 and *Eubranchus* sp. 2 of Behrens and Hermosillo (2005), both known only from La Jolla, California), but none is known solely from the northern SCB like *F. goddardi* (see range information in Behrens and Hermosillo, 2005).

Flabellina goddardi appears to specialize on colonies of a single species of *Bougainvillia*-like hydrozoan, and, indeed, the regeneration of cerata and overall growth of the specimen we held for six days following a bout of feeding on this hydroid suggests this species is high quality prey for the aeolid. Other aeolid nudibranchs, including species of *Flabellina*, have been previously recorded feeding on species of *Bougainvillia* (McDonald and Nybakken, 1997).

The occurrence of *F. goddardi* in the spring to early summer matches that of other small aeolid and dendronotacean nudibranchs in California and Oregon (Bertsch et al., 1972, Table 5; Nybakken, 1974; personal observations) and corresponds with seasonal new growth of many hydroid species in the region (personal observations).

The three specimens of *F. goddardi* found at Anacapa Island in April, 2016 were found in an area of 0.09 m^2, along with two specimens of *F. trilineata* (Figure 11), and owing to the similarities in color pattern, were initially identified as the latter species (D. Klug, personal communication to JG, 11 May 2016). Reasoning that *F. goddardi* could have been identified as *F. trilineata* before, we searched on Google for "*Flabellina trilineata*, Anacapa Island," and found not only an additional example of the same misidentification, but that the specimen photographed had been found more than two years prior to the discovery of the type specimen of *F. goddardi* in May 2008 (Segal, 2011). Additional searches for images of *F. trilineata* from southern California, including on the Sea Slug Forum (http://www.seaslugforum.net/showall/flabtril), Divebums Species Database (http://species.divebums.com/index.php?l=sciname&n=Flabellina%20trilineata), and Flickr (https://www.flickr.com/search/?text=flabellina%20trilineata&view_all=1) did not reveal any more specimens identified as *F. goddardi* (nor any additional locality records).

The most obvious external differences between *F. goddardi* and *F. trilineata* are that *F. goddardi* has smooth rhinophores, a longer and much more extensible tail than *F. trilineata*, and longer cephalic tentacles. These morphological differences aside, the similarity in color pattern between the two species is striking, especially at Anacapa Island, where the subapical red band on the cerata of *F. goddardi* grades into orange and extends farther down the cerata than seen in most specimens from the mainland (Figure 10). This resemblance raises the possibility of mimicry between the two species. Two other nudibranchs found subtidally at Anacapa Island, the dorid *Limacia cockerelli* (MacFarland, 1905) (Figure 12) and the aeolid *Austraeolis stearnsi* (Cockerell, 1901) (Figure 13), have dorso-lateral appendages (papillae and cerata, respectively) similar in color to the cerata of *F. goddardi* and *F. trilineata*, and their rhinophores are also similar in coloration to those of *F. trilineata* (Figure 11). Some or all of these four species may form a Müllerian mimicry complex as a defensive adaptation against predatory fish.

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A multiple microsatellite assay to evaluate the mating behavior of the intensively exploited marine gastropod *Concholepas concholepas* (Bruguière, 1789) (Gastropoda: Muricidae)

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ABSTRACT

The study of reproduction and mating beahavior constitutes a main issue in biology, ecology and evolution, given its relation with fitness traits. Here, we developed a simple microsatellite multiple assay to evaluate the mating strategy and male reproductive success of the marine gastropod *Concholepas concholepas* (Bruguière, 1789), an important fishery resource and a key predator species of Chilean rocky shore communities. *Concholepas concholepas* is a dioecious species with internal fertilization, encapsulation, and long larval phase. In laboratory, adult males and females were cultivated in tanks, and 37 larvae from 5 different clutches were genotyped to run paternity analyses using seven microsatellite loci. Results showed that promiscuity is a common mating behavior in *C. concholepas* displaying an exceptionally high level of multipaternity and males participating as fathers in clutches from more than one female. This microsatellite multiple assay helped to improve our understanding of the reproductive beahavior of this ecological key species with high economic importance.

INTRODUCTION

Given its importance in determining fitness, studying reproductive success is crucial to understanding an organism's biology (Stearns, 2000; Avise et al., 2011). Also, the study of the reproductive strategies of commercially relevant species is crucial for developing appropriate conservation and management policies (Defeo and Castilla, 2005; Hobday et al., 2010). One of the main challenges in estimating reproductive success in sexual species is determining an accurate method to quantify reproductive success; this is especially challenging for males. Here, we developed a simple multiple microsatellite assay to study the reproductive strategy and the reproductive success of the marine gastropod *Concholepas concholepas* (Bruguière, 1789) (Figure 1). *Concholepas concholepas* is locally known as "loco" and is one of the main target species of small-scale artisanal fisheries operating along the southeastern coast of Chile (Defeo and Castilla, 2005). We first tested a set of previously developed microsatellite loci for use in paternity analyses. Secondly, we inferred some general aspects of the mating behavior of this species.

MATERIALS AND METHODS

Analyses were run on mature adult individuals obtained from a single 50 L tank containing an experimental aggregation of 18 females and 35 males. Individuals were sexed following methodologies described by Castilla (1974). All of the reared individuals used in this study were sexually mature and capable of mating (Manríquez et al., 2008). From this experimental aggregation, five clutches laid by five females identified as potential mothers were studied. Between five and 11 veliger larvae pre-hatching from one or two ovicapsules were collected at random, and the paternity of each clutch analyzed. When two ovicapsules were sampled, larvae from the two capsules were mixed before

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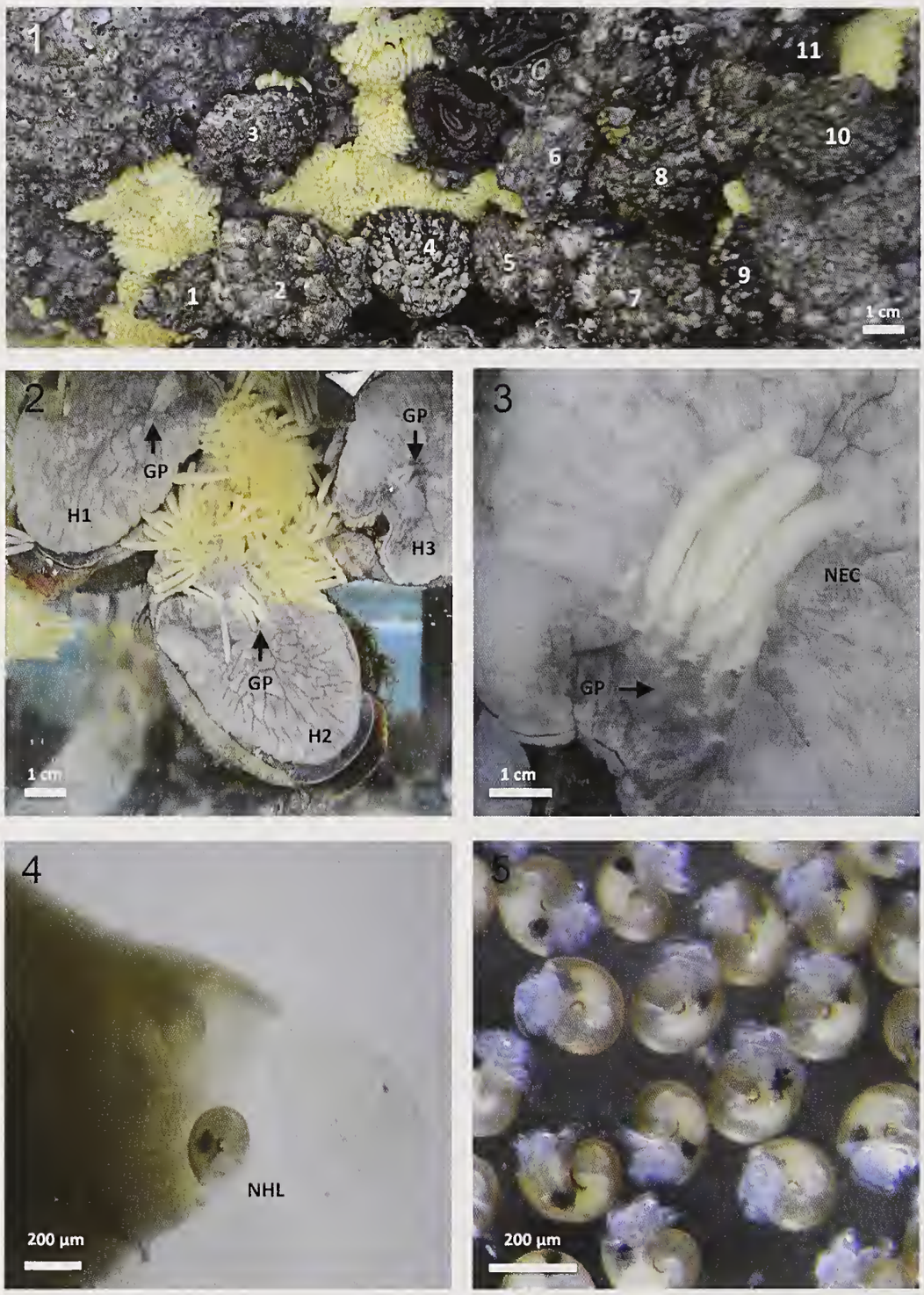

Figures 1–5. *Concholepas concholepas*. **1.** Group of several individuals (n=11) laying egg capsules on the rocky shore during low tide in nothern Chile. **2.** Group of three females laying egg capsules on the inside of a glass aquarium. **3.** Clutch of newly laid egg capsules close to the gonadal pore. **4.** Newly hatched veliger larvae leaving the apical aperture of a mature egg capsule. **5.** Group of newly hatched larvae 5 min after being released. Abbreviations: H1–3: female individuals; GP: gonadal pore; NEC: newly laid egg capsules; NHL: newly hatched larvae.

choosing which would be analyzed. Simultaneously, a small piece of the muscular foot tissue (less than 1 cm^3) was removed from each adult individual of the experimental aggregation.

DNA extraction for adults was performed using the E.Z.N.A.® Tissue DNA kit (OMEGA) following the manufacturer's protocol. To each larva we added 200 µL of 5% Chelex solution and 2 µL of proteinase K (0.2 mg/mL). Then, this mixture was incubated at 56°C for 2 hours followed by 8 minutes at 100°C. A total of 37 veliger larvae (from 6 ovicapsules) were successfully genotyped. We selected seven microsatellite loci (Cc2A11-1, Cc1D8,

Table 1. Summary statistics of the microsatellite loci used for the paternity analysis of *Concholepas concholepas*. Locus name, number of individuals genotyped at the specific locus (N), number of observed alleles (Na), and unbiased expected genetic diversity (He) are indicated for each locus; adults and larvae were used for calculations. The table shows the probability of the exact test for Hardy-Weinberg equilibrium (PHW) and the probability of exclusion (P_{excl} of 95% confidence level) defined as the probability of excluding a randomly chosen unrelated candidate parent from the parentage analysis.

Locus	N	Na_{tot}	Na_{adult}	Na_{larvae}	He_{adult}	He_{larvae}	PHW	P_{excl}
Cc2A11-1	94	13	13	12	0.688	0.782	0.036	0.779
Cc1D8	95	26	24	19	0.873	0.903	0.908	0.943
Cc1E5	94	13	12	11	0.850	0.816	0.073	0.868
Cc2A5	95	13	12	9	0.642	0.459	0.444	0.618
Cc709	95	8	8	7	0.702	0.775	0.271	0.741
CcQVC	90	10	10	7	0.835	0.806	0.548	0.831
Cc1H2	91	58	51	32	0.974	0.946	0.023	0.993
TOTAL	95	159	144	112	0.806	0.793	0.034	0.999

Cc21E5, Cc2A5, Cc1H2, Cc709 and CcQVC) previously developed to study the spatial population genetics of loco (Cárdenas et al., 2007, 2011). The criteria to select loci were: (1) level of polymorphism, (2) repeat motif and (3) amplification pattern. Although amplification patterns were unambiguous, we checked the microsatellite data for evidence of null alleles and technical artifacts such as stuttering and large allele dropout using MICRO-CHECKER 2.2.3 (Van Oosterhout et al., 2004). Genetic diversity analyses of larvae and adults were performed using Genetix v. 4.05 (Belkhir et al., 2004). Tests for genotypic linkage disequilibrium and genetic differentiation were computed using Genepop v. 3.3 (Raymond and Rousset, 1995).

Paternity analyses as well as estimations of the expected probability of exclusion of each locus and across loci were performed using the software CERVUS 2.0 (Marshall et al., 1998). This procedure employs maximum likelihood calculations previously proposed by Meagher (1986). Given the genotypes of the embryos and the known genotype of the mother, paternity was assigned to the male in the tank with the highest log-likelihood ratio (LOD). In order to take into account potential misidentifications of sex, the remaining 53 individuals in the aquarium were considered as potential fathers. One advantage of using CERVUS 2.0 is the possibility to evaluate the statistical significance of the LOD through computer simulations (here 95% confidence level; Marshall et al., 1998). Computations were carried out using 10,000 iterations of the population allelic frequencies estimated using the genotypes of the 53 adults studied. We estimated the number of potential fathers per clutch and whether or not a single male individual participated in more than one brood. Posteriorly, we estimated the level of relatedness between all of the adults (males and females) in the tank using the ML relate software (Kalinowski et al., 2006).

RESULTS AND DISCUSSION

Throughout the entire dataset, we found that none of the loci showed preferential amplification of short alleles or any evidence of scoring errors or linkage disequilibrium. All loci were highly polymorphic with 159 alleles detected in the 53 adults inspected and 112 alleles detected in the 37 larvae analyzed (Table 1). After Bonferroni corrections, no significant deviations from Hardy-Weinberg equilibrium were observed. Altogether, the probability of exclusion of the seven loci was 0.999, and the probability of exclusion was high for each of the seven loci analyzed (Table 1).

From a total of 37 larvae examined, 34 (91.9%) were unequivocally assigned to only one adult present in the aquarium. In the remaining cases, analyses could not discriminate between two males as potential fathers. The paternity analysis showed that a total of 18 out of 35 males (51.4%) participated in the clutches as fathers (Table 2). The number of sires per clutch ranged from three to seven, and the number of fertilized females per sire ranged from one to three (Table 2); additionally, sire M19 had the highest percentage of assignments, and this was achieved with two different female mates (Table 2). In general, the relatedness analysis indicated a wide range of kinship between adults in the aquarium. Most adults were not related (relatedness level = 0). However, some pairs of individuals were identified as potential half siblings (relatedness level close to 0.25), and in two cases, some evidence of parental relationship was detected (relatedness level close to 0.5). With the exception of one case in which half siblings were identified, the potential mates assigned by parentage were not related.

In summary, the seven loci selected here were highly useful to perform parentage analyses in *C. concholepas*. We found evidence of promiscuity and a high level of multiple paternity in this species which is in concordance with reports for other gastropod species (Dupont et al., 2006; Mäkinen et al., 2007; Brante et al., 2011; Xue et al., 2014). In addition, 94.4% of males that participated as fathers contributed in more than one brood. From the information presented here, it will be possible to design new experiments using the present multiplex microsatellite assay to fully understand the mating behavior and reproductive strategy of *C. concholepas*.

Table 2. Parental assignments of *Concholepas concholepas* veliger larvae. *Ncap* = Number of ovicapsules analyzed; *Nlar* = Total number of larvae analyzed; *Nsires* = Number of sires assigned to each female. Also, the code of each male and the number of larvae assigned for each female is presented.

	Ncap	*Nlar*	*Nsires*	M-H3	M4	M7	M8	M9	M10	M1	M12	M16	M17	M19	M20	M22	M24	M33	M35	M39	M42	Not assigned
Female 1	1	5	5						1	1		1	1				1					
Female 2	1	5	3							1	1		1									2
Female 3	1	9	7		1	1		1				1		2						1	1	1
Female 4	2	11	7	1	1		1							2	2	1		3				
Female 5	1	7	6	1	1											2	1		1	1		
TOTAL	**6**	**37**	**18**	**2**	**3**	**1**	**1**	**1**	**1**	**2**	**1**	**2**	**2**	**4**	**2**	**3**	**2**	**3**	**1**	**2**	**1**	**3**

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Ancistrolepidine gastropods (Buccinidae) from the upper Eocene hydrocarbon seep deposits in Hokkaido, northern Japan

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ABSTRACT

Two ancistrolepidine gastropods, *Ancistrolepis modestoideus* (Takeda) and *Bathyancistrolepis mikasaensis* new species are described from the upper Eocene seep carbonates of the Poronai Formation in Mikasa City, central Hokkaido. One specimen of *Ancistrolepis* sp. resembling *A. grammatus* (Dall) co-occurred with *Conchocele bisecta* (Conrad) is also described from the upper Eocene Sakasagawa Formation in Tomamae Town, northwestern Hokkaido. These species constitute the oldest to date record of the genera *Ancistrolepis* and *Bathyancistrolepis*. Time of the first appearance of ancistrolepidine gastropods in the North Paeific corresponds with the increasing number of hydrocarbon seep sites, which could have affected to accelerated diversification of deep-sea buccinids in the North Pacific.

Additional Keywords: Eocene, Gastropoda, new species, Ancistrolepidinae

INTRODUCTION

Most Recent ancistrolepidine gastropods are deep-shelf dwellers and distribution of fossil and modern species is confined to the northern Pacific, except for one Recent species *Ancistrolepis vietnamensis* Sirenko and Goryachev, 1990 from the South China Sea (Tiba and Kosuge, 1981, 1982; Titova, 1993, 1994; Egorov and Barsukov, 1994; Higo et al., 1999; Kantor and Sysoev, 2006; Gulbin, 2009). Habe and Sato (1973) originally included five genera into the subfamily "Ancistrolepisinae": *Ancistrolepis* Dall, 1895; *Bathyancistrolepis* Habe and Ito, 1968; *Clinopegma* Grant and Gale, 1931; *Neancistrolepis* Habe and Sato, 1973; and *Pseudoliomesus* Habe and Sato, 1973. However, the generic composition and status of Ancistrolepidinae remains somewhat controversial (see Amano et al., 1996 for discussion). Moreover, the genus *Ancistrolepis* was subdivided into *A. eucosmius* and *A. grammatus* stocks, based on their size and condition of spiral cords (Gladenkov et al., 1988; Titova, 1993; Amano et al., 1996). In this paper, we adopt the systematic treatment of genera following Amano et al. (1996).

Genera *Ancistrolepis* and *Bathyancistrolepis* first appeared in the late Eocene and constitute the oldest record among the subfamily (Titova, 1993). These earliest representatives of the subfamily are important for the reconstruction of the evolution of the entire subfamily Ancistrolepidinae. Currently, two species of the genus *Ancistrolepis* and one species of the genus *Bathyancistrolepis* species have been recovered from the upper Eocene deposits in central and northwestern Hokkaido, northern Japan. At least one of the *Bathyancistrolepis* species is new to science. This article describes these species and discusses their evolutionary significance.

MATERIALS AND METHODS

Five specimens of *Ancistrolepis modestoideus* (Takeda, 1953) and two specimens of *Bathyancistrolepis mikasaensis* new species were obtained from the seep carbonates included in mudstones of the upper Eocene Poronai Formation located at 200 m west of the mouth of Yayoi Banno Creek, Yayoi Town in Mikasa City, central Hokkaido (Figure 1, Loc. 1; 43°15′34″ N, 141°55′54″ E). The thyasirid *Conchocele bisecta* (Conrad, 1849), the vesicomyid *Hubertschenckia ezoensis* (Yokoyama, 1890), the carditid *Cyclocardia tokudai* (Takeda, 1953) were also recorded by Amano and Jenkins (2007) from the same locality. One specimen of *Ancistrolepis* sp. was collected from the upper Eocene Sakasagawa Formation at the cliff along the Kotanbetsu River, 2 km west of Seiryu Bridge in Kiritachi, Tomamae Town, northwestern Hokkaido (Figure 1, Loc. 2 = Loc. SK 15 of Noda, 1992; 44°13′22″ N, 141°53′8″ E) by Mr. Futoshi Akamatsu (Shunan City, Yamaguchi Prefecture). The same silty sandstone also contains multiple articulated specimens of *Conchocele bisecta*. Abbreviation used is: JUE, Joetsu University of Education, Joetsu, Niigata Prefecture, Japan.

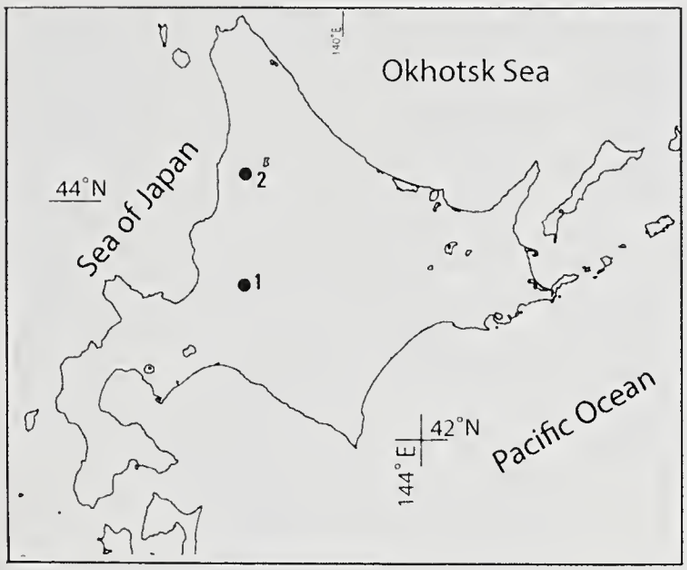


Figure 1. Locality map of the ancistrolepidine gastropods examined in this study.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Buccinidae Rafinesque, 1815
Subfamily Ancistrolepidinae Habe and Sato, 1973

Remarks: The subfamily name was originally proposed as Ancistrolepisinae. This was still used as the original name by Bouchet and Rocroi (2005), Kantor and Sysoev (2006) and Gulbin (2009). However, the stem of the word *Ancistrolepis* is *Ancistrolepid-* and should be correctly used as Ancistrolepidinae (see Goryachev, 1987). Although the paper by Habe and Sato (1972) was actually published in February, 1973, not in November, 1972 (see Habe, 1973), some authors have mistaken the date of this publication as 1972 (Gladenkov et al., 1988; Titova, 1993; Egorov and Barsukov, 1994; Amano et al., 1996).

Genus *Ancistrolepis* Dall, 1895

Type Species: *Chrysodomus eucosmius* Dall, 1891

***Ancistrolepis modestoideus* (Takeda, 1953)**
(Figures 2–4, 6)

Neptunea modestoidea Takeda, 1953: 53–54, pl. 3, 1–7, pl. 5, fig. 8; Matsui, 1958: 6, pl. 30, figs.1a, b; Honda, 1989: 102.
Ancistrolepis modestoideus (Takeda).—Oyama et al., 1960: 60, pl.8, figs.5a–d.
Ancistrolepis (*Ancistrolepis*) *modestoideus* (Takeda).—Titova, 1993: fig. 2I.

Material Examined: Among five specimens from the Poronai Formation, three specimens are deformed (JUE no. 15941, 15942). All specimens lack early whorls.

Remarks: The type locality of this species was from the Maoka Group in southwestern Sakhalin, correlated with the upper Eocene Poronai Formation in Hokkaido (Takeda, 1953). Titova (1993, p. 4, Fig 2I) illustrated one specimen as *A.*(*A.*) *modestoideus* from the upper Eocene Takaradai Formation along the Tomari River in southwestern Sakhalin. Although Oyama et al. (1960) allocated this species to the genus *Ancistrolepis*, Honda (1989) assigned it to the genua *Neptunea* Röding 1798. However, when Honda (2000) described a new species of *Ancistrolepis* from the lower Oligocene Iwaki Formation in Fukushima Prefecture, he mentioned this species as *Ancistrolepis* (*A.*) *modestoideus*. A Paratype specimen of *A. modestoideus* was illustrated from the Yayoi coal mine near the locality from where we collected the specimens described herein.

Specimens of *A. modestoideus* collected by the senior author are characterized by smaller shells (up to 32.3 mm in height), four rounded whorls with five to eight spiral cords on the penultimate whorl and more than ten cords on body whorl. Spiral cords are prominent, but rounded and separated by wider interspaces. Overall shape and details of spiral sculpture are consistent with other authors' description of this species from Japan and Sakhalin.

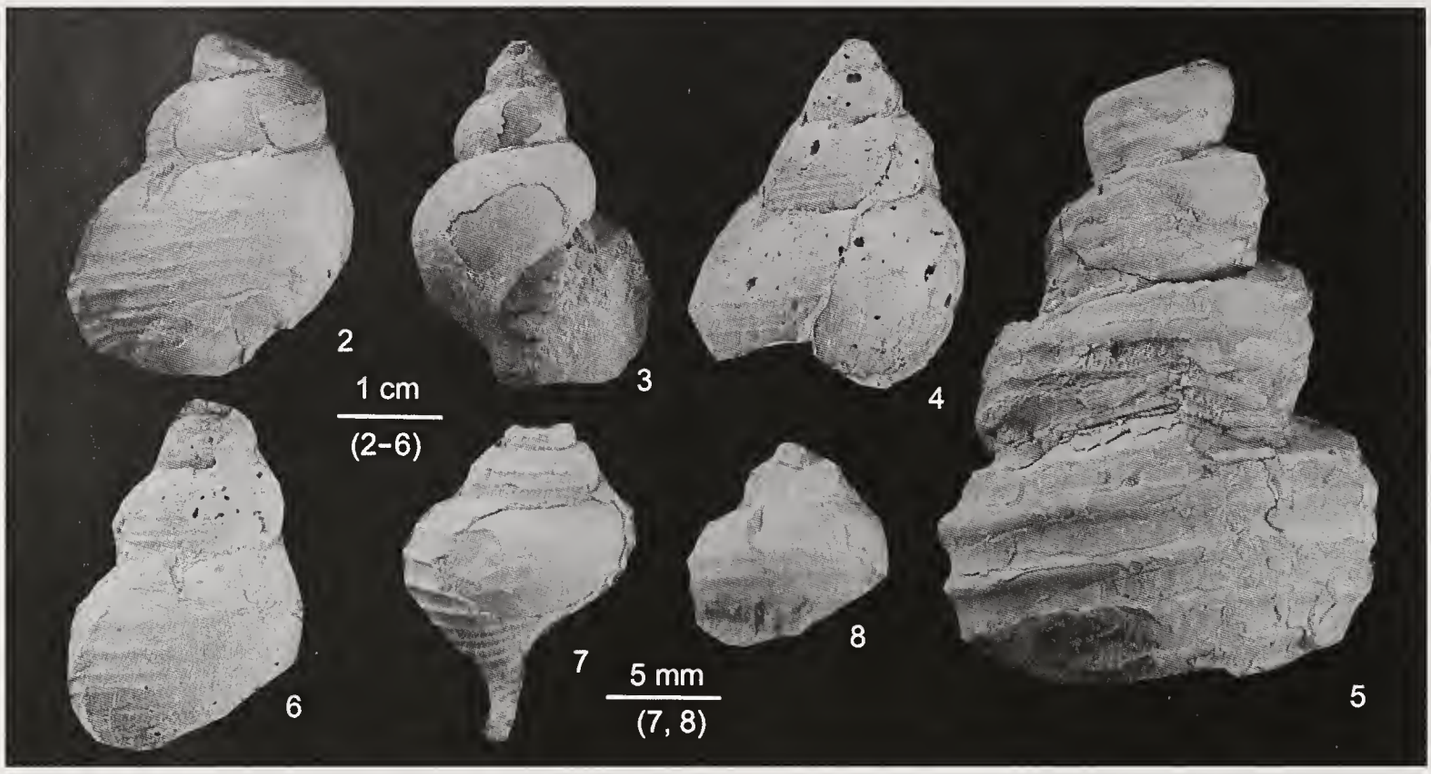
Distribution: Upper Eocene Maoka Group and Takaradai Formation in southwestern Sakhalin, Poronai Foramtion in central Hokkaido. Lower Oligocene Charo and Nuibetsu Formations in eastern Hokkaido.

***Ancistrolepis* sp.**
(Figure 5)

Material Examined: One incomplete and deformed specimen (JUE no. 15943) from the Sakasagawa Formation at Kiritachi is examined. The specimen is missing early whorls.

Description: Shell slightly deformed, moderate in size (shell height, 53.2 mm+; diameter, 38.6 mm), more than four whorls. Shoulder angulated with flat area above shoulder. Shell material mostly dissolved, but surface sculptured with five prominent spiral cords on penultimate whorl and more than ten cords on last whorl, separated by wider interspaces.

Remarks: This species resembles the Recent species, *A. grammatus* (Dall, 1907) in having a sharply angulated shoulder, a flat subsutural area above shoulder, similar number of prominent spiral cords (five to six cords on penultimate whorl and nine to twelve on body whorl in *A. grammatus*; Okutani, 2000). However, this species is much smaller than the Recent species. Recent specimen from off Kurile Islands deposited at JUE attains 128 mm in shell height.



Figures 2–8. Ancistrolepidine gastropods studied in the paper. **2–4, 6.** *Ancistrolepis modestoideus* (Takeda, 1953). **2, 6.** adapertural view, JUE no. 15942, Loc. 1; **3.** apertural view, JUE no. 15491. **4.** adapertural view of the silicon rubber cast of JUE no. 15941, Loc. 1. **5.** *Ancistrolepis* sp., adapertural view, JUE no. 15943, Loc. 2. **7, 8.** *Bathyancistrolepis mikasaensis* new species. **7.** Holotype, adapertural view, JUE no. 15944, Loc. 1. **8.** Paratype, adapertural view, JUE no. 15945, Loc. 1.

Ancistrolepis jimgoederti Moore, 1984 from the upper Oligocene part of the Lincoln Creek Formation in southwestern Washington is similar to the Kiritachi species in having a flat subsutural area above the shoulder. However, *A. jimgoederti* differs from *Ancistrolepis* sp. in being larger (up to 70 mm in height) and having fewer T-shaped spiral cords (only four on penultimate whorl).

Distribution: Upper Eocene Sakasagawa Formation in northwestern Hokkaido.

Genus *Bathyancistrolepis* Habe and Ito, 1968

Type Species: *Clarysodomus trochoideus* Dall, 1907

Remarks: Species in this genus can easily be separated from *Ancistrolepis* by their small and ovate shell with low spire. However, some authors treated this genus as a subgenus of *Ancistrolepis* (Tiba, 1981; Titova, 1993; Egorov and Baruskov, 1994). Its representatives live in deep water (100 to 2000 m; Okutani, 2000) from Kumano-nada to the southern Kurile Islands (Okutani, 2000; Kantor and Sysoev, 2006).

Bathyancistrolepis mikasaensis new species
(Figures 7, 8)

Diagnosis: A small-sized *Bathyancistrolepis* species sculptured with three spiral cords on the penultimate whorl and eleven on last whorl.

Description: Shell small-sized, attaining 12.5 mm in height, thin, ovate, with three whorls, protoconch and juvenile whorls missing. Subsutural groove very narrow and deep; shoulder rounded. Last whorl is inflated, occupying approximately 86% of shell height; spire very low. Surface of penultimate whorl is sculptured with three sharp spiral cords and separated by very wide interspaces; last whorl above shoulder with three sharp cords and base with eight cords separated by wider interspaces. Siphonal canal short and rather straight, without fasciole.

Type Material: Holotype, JUE no. 15944 (Shell height 12.5 mm+; diameter 10.0 mm); Paratype, JUE no. 15945 (Shell height 8.0 mm+; diameter 8.3 mm)

Type Locality: The cliff along the Ikushunbetsu River at 200m west of the mouth of Yayoi Banno Creek, Yayoi Town in Mikasa City, central Hokkaido.

Remarks: The new species differs from the Eocene species, *Bathyancistrolepis sitakaraensis* (Matsui, 1958) in having a smaller size (maximum shell height of *B. sitakaraensis*, 38 mm), lower spire, and in lacking interstitial threads between cords.

The Recent species, *B. trochoideus* (Dall, 1907) can be easily separated from the new species by its larger shell (up to 36 mm in height) with some interstitial threads between main spiral cords and a strongly twisted siphonal canal.

Etymology: The new species is named for the city from where the type material was collected.

Distribution: Known only from the type locality, upper Eocene Poronai Formation, Mikasa City, eastern Hokkaido.

DISCUSSION

The three described species probably lived at or in the vicinity of methane seeps. In the Poronai site (Loc. 1), two ancistrolepidine gastropods occurred in the carbonate indicating relatively low $\delta^{13}C$ value (+5.8 to −44.7‰; Amano and Jenkins, 2007). Moreover, they are co-occurring with abundant bivalve species with living counterparts known to host symbiotic chemoautotrophic bacteria and living at or in the vicinity of methane seeps, such the thyasirids *Conchocele bisecta* (Conrad, 1849) and the vesicomyid *Hubertschenckia ezoensis* (Yokoyama, 1890). In the Kiritachi site, although no isotopic data is available, multiple *C. bisecta* co-occurred gregariously with *Ancistrolepis* sp. The occurrence of *Ancistrolepis* in association with inferred methane seep-dwelling mollusks is not unique in the North Pacific. A North American species, *Ancsitrolepis teglandae* (Weaver, 1942) was found in the same assemblage with the vesicomyid *Calyptogena katallaensis* (Kiel and Amano, 2010) in the lower Oligocene Kulthieth Formation in Katalla district, southern Alaska (Kiel and Amano, 2010). These Paleogene occurrences are very similar to well-documented Miocene seep sites in Japan. From the middle Miocene Akanuda Limestone (Bessho Formation, Nagano Prefecture, central Honshu), *Ancistrolepis koyamai* (Kuroda, 1931) was described by Tanaka (1959), originally as a species of *Buccinum*, and was found co-occurring with *Conchocele nipponica* (Yabe and Nomura, 1925), and *Adulomya uchimuraensis* Kuroda, 1931. *Clinopegma* aff. *borealis* Tiba, 1969 has been recorded from the seep carbonates of the upper Miocene Morai Formation, co-occurring with *Conchocele bisecta* and *Calyptogena pacifica* Dall, 1891 (Amano, 2003). Very recently, the modern species *A. grammatus* has been found from the deep sea (778 m) off the Paramushir Island, close to the methane seep site with *C. bisecta* (Gulbin and Ivin, 2015). Judging from the isotope record and associated fauna, the Paleogene occurrences of ancistrolepidine gastropods are similar to both modern and Miocene.

As mentioned above, the genus *Ancistrolepis* was subdivided into two stocks: *A. eucosmius* (Dall, 1891) and *A. grammatus* (Dall, 1907) by Titova (1993). Moreover, two groups were recognized by Titova (1993) within the *A. grammatus* stock: *A. modestoideus-A. macneili* and *A. grammatus* groups. The first group is characterized by a rounded shoulder and absence of the T-shaped spiral cords while the second group, including *A. grammatus* has a flat or concaved area above the shoulder and T-shaped cords. The oldest known species of the second group was *A. jimgoederti* Moore, 1984 from the upper Oligocene part of Lincoln Creek Formation (See Titova, 1993). However, *Ancistrolepis* sp. from the upper Eocene Sakasagawa Formation at Kiritachi belongs to the *A. grammatus* species group as described above. Titova (1993) included *A.* aff. *modestoideus* as the oldest species of *A. grammatus* stock from the upper Eocene Takaradai Formation in southwestern Sakhalin into *A. modestoideus-A. macneili* group. As *A. grammatus* group appeared at the same time as *A. modestoideus-A. macneili* group, it is possible to separate these groups as independent stocks.

Titova's classification of *Bathyancistrolepis* is somewhat confusing. Some of the species should be included in *Ancistrolepis* on the basis of their high spire and moderately inflated last whorl. The following species should be included in *Ancistrolepis grammatus* stock: the Oligocene species, *A. chikuzenensis* (Nagao, 1928), the Miocene species, *A. togariensis* Naruse, 1952 and *A. miensis* Araki, 1960. The Miocene species, *A. striatus* Kanno, 1958 and the Plio-Pleistocene species, *A. masudaensis* Nomura, 1937 should be in the *A. eucosmius* stock, as pointed out by Amano et al. (1996). Consequently, the currently known species of *Bathyancistrolepis* include *B. sitakaraensis*, *B. eguchii* (Kamada, 1962), *B. trochoideus*, and *Bathyancistrolepis mikasaensis* new species. As suggested by Kantor and Sysoev (2006), *B. trochoideus tokoyodaensis* Ozaki, 1958 and *B. trochoideus ovoideus* (Habe and Ito, 1965) are synonyms of *B. trochoideus*. The earliest species of the genus *Bathyancistrolepis* are *B. sitakaraensis* and *B. mikasaensis* new species from the upper Eocene formations in Hokkaido.

Buccinid gastropods including the family Ancistrolepidinae had rapidly diversified and spread geographically within the North Pacific since the late Eocene (Titova, 1993, 1994). The proposed reason for that change, traditionally involved climatic deterioration that started at the end of the Eocene (Titova, 1993). Shallow-marine gastropods in general were changing stepwise, from predominantly cosmopolitan to more locally distributed taxa (Oleinik and Marincovich, 2003). How climatic cooling accelerated the diversification and spread of the Buccinidae remains uncertain. It is at the same time, during the late Eocene, when Ancistrolepidinae are found associated with the hydrocarbon seep sites.

The Cenozoic-type seep taxa such as vesicomyids and bathymodiolines first appeared in the middle Eocene of the northern Pacific and significantly expanded their geographic ranges in the late Eocene (Amano and Kiel, 2007; Amano and Jenkins, 2011; Kiel and Amano, 2013). From the middle Eocene onward, the number of seep-bearing formations suddenly and significantly increased (Kiel, 2009). The origin of Cenozoic-type seep molluscan taxa was, therefore, attributed to the increase of a sulfate concentration in the ocean at the middle Eocene (Kiel, 2015). The ancistrolepidine gastropods examined in this study have been found in upper Eocene hydrocarbon seep deposits. Ancistrolepidinae are carnivorous gastropods and probably fed on the fauna in the seep sites, just

like their modern counterparts do. Recent buccinids such as *Ancistrolepis grammatus*, *Neptunea* spp., *Buccinum* spp., *Calliloncha* spp., *Eosipho* spp., and *Kryptos* spp. have been found in modern seep sites (e.g. Warén and Bouchet, 2001; Okutani and Iwasaki, 2003; Levin, 2005; Fujikura et al., 2008; Fraussen and Sellanes, 2008). As opportunistic feeders, species from these genera were also found at modern non-seep localities. In fact, the majority of the late Eocene and Oligocene occurrences of Ancistrolepidinae from Kamchatka and Sakhalin are also from non-seep deposits. The earliest occurrence of the genera *Ancistrolepis* and *Bathyancistrolepis* at the late Eocene hydrocarbon seep sites suggests that they adapted seeps as their habitat shortly after their first appearance in the fossil record. Similar rapid adaptation for hydrothermal seep habitats were recorded for serpulid polychates (Vinn et al., 2013). Moreover, modern species of Ancistrolepidinae are larger than the Eocene species. Similar trends are observed within vesicomyids and bathymodiolins (see also Amano and Kiel, 2007; Kiel and Amano, 2013). These observations may indicate that the documented late Eocene increase in the seep sites in the North Pacific and worldwide, provided ancistrolepidine gastropods with an additional food resource and helped facilitate their dispersal in the northern circum-Pacific.

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Parachondria joyeuse: a peculiar new species of Hispaniolan Annulariidae (Gastropoda: Littorinoidea)

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ABSTRACT

Parachondria joyeuse is described from the eastern Dominican Republic. The new species is characterized by a thin, high-spired, nearly smooth shell and a peculiar color pattern. It is placed in *Parachondria* with reservation.

INTRODUCTION

Bartsch's 1946 review of the Hispaniolan Annulariidae is the most comprehensive account of the family thus far published. However, examination of his sites reveals that Bartsch and the many collectors from whom he obtained material had very few collections from the eastern third of the island. In the 1960s and 1970s, Fred Thompson and his colleagues from the Florida Museum of Natural History made numerous collections in these unstudied areas. The results of these efforts are now being published (Watters, 2013; 2016; and others). They indicate an unexpected wealth of new taxa and morphological diversity largely endemic to small areas of the island. Abbreviations used are: GTW: G. Thomas Watters collection; UF: Florida museum of Natural History, Gainesville, Florida.

SYSTEMATICS

Family Annulariidae Henderson and Bartsch, 1920

Genus *Parachondria* Dall, 1905

Type Species: *Turbo fascia* Wood, 1815, by original designation.

***Parachondria joyeuse* new species**
(Figures 1–7)

Description: Shell thin, fragile, high-spired for family; spire ca. 3 × the length of aperture. Holotype 14.1 mm length. Largest adult specimen seen: 16.7 mm length including lip (paratype 1), smallest 14.1 mm length including lip (holotype). Protoconch wholly or partially lost in most adults, consisting of 1.5 minute, smooth whorls, not clearly delimited from teleoconch, white with tan spot on apex. Teleoconch of ca. 5.75 rounded whorls. Axial sculpture of teleoconch present only as microscopic, close-set ridges on first 3–4 whorls, becoming much weaker to obsolete on remainder of whorls; numerous fine, close-set growth lines apparent. Spiral sculpture of ca. 30 very weak, low, subequal, rounded cords. Umbilicus bounded by weak ridge with smaller cord or ridge within umbilicus. Suture simple, without tufts or serrations, not channeled. Aperture teardrop-shaped. Lip single, narrowly expanded, narrowest facing the umbilicus, weakly auriculate posteriorly, scarcely solute from previous whorl. Color pattern variable: from white and unpatterned to boldly patterned. Pattern of ca. 7 brown, smudged, spiral bands broken into axially aligned blotches. One band bounds umbilicus, another broader band may occur within umbilicus. Early teleoconch whorls usually not banded. Bands persist over both sides of lip. Operculum paucispiral and corneous with outer granular, calcareous deposit. Radula and anatomy unknown.

Type Material: Holotype, UF 216406, 14.1 mm length; four paratypes, all UF 505262: paratype 1, 16.7 mm length; paratype 2, 15.9 mm length; paratype 3, 15.9 mm length (subadult); paratype 4, 10.6 mm length (subadult); all from type locality.

Other Material Examined: Total of 35 specimens distributed as: UF 505263, 19 specimens, including type material, all from type locality; UF 216418, one specimen, from type locality; UF 216731, 10 specimens, 13 km NW of Sabana Grande de Boya, Monte Plata Province; GTW 16522a, five specimens, 321 m elevation, mesic limestone bluffs behind cemetery, Las Flores (suburb of Majagual), Monte Plata Province, 19.0397° N, -69.8390° W.

Figures 1–7. *Parachondria joyeuse* new species. All from type locality. **1, 2.** Holotype, UF 216406, 14.1 mm length. **3–6.** Paratypes, UF 505262. **3.** Paratype 1, 16.7 mm length. **4.** Paratype 3, 15.9 mm length. **5–6.** Paratype 2, 15.9 mm length. **7.** Operculum.

Type Locality: 200 m elevation, 1 km W of Majagual, Monte Plata Province, Dominican Republic.

Distribution: Known only from the region of Majagual. This area is in the Sierra de El Seibo, a detached portion of the Cordillera Central, in the Los Haitises Limestone.

Habitat: Specimens have been found at the base of limestone knolls in mesic vegetated areas and pastures. None of the specimens were collected alive and only one still retained an operculum.

Etymology: "Joyeuse" (French, joyous) was the sword of Charlemagne, a reference to the shape and beauty of the shell and it's variability of color. In the 11th century poem *La Chanson de Roland* Joyeuse is described as "never was there a sword to match it; its colour changed thirty times a day." "Joyeuse" is used as a noun in apposition.

Remarks: The "polka dot" pattern on a high-spired shell is shared by several otherwise unrelated and geographically distant Hispaniolan annulariids: the *Chondropoma* (*Wetmorepoma*) complex from the Barahona Peninsula, *Crossepoma emilianum* (Weinland, 1862) from the western Tiburon Peninsula of Haiti, and particularly *Diplopoma laferrierense* (Bartsch, 1946) from La Ferrière, Haiti, and *Diplopoma elegantissimum* (Bartsch, 1946) from Saltrou (now Belle-Anse), Haiti. All of these substantially differ from *P. joyeuse* in sculpture and apertural details, particularly in the absence of sutural tufts in *P. joyeuse*. *Diplopoma* also differs in having a spiral lamella on the operculum. The sculpture is somewhat similar to that found in *Samanicola*, another very unusually sculptured genus, but the features of the aperture are very different. In *Samanicola* the lip is double, widely expanded, and adnate; in *P. joyeuse* it is single, narrowly expanded, and solute. *Samanicola* is associated with the Samaná Peninsula and *P. joyeuse* occurs at adjacent Majagual in the Sierra de El Seibo.

This species is placed in *Parachondria* with reservation. That genus (with a Jamaican type species) is currently a catch-all grouping that undoubtedly contains numerous distinct phylogenetic groups. *Parachondria joyeuse* is similar in its overall sculpture to the *Chondropomorus* subgenus of *Parachondria*, the Hispaniolan members of which were reviewed by Watters (2016). But the sculpture of *P. joyeuse* is microscopic and lacks any evidence of sutural tufts; the peculiar color pattern does not occur in other members of *Chondropomorus*. Further study, including phylogenetic work, will probably necessitate the recognition of a separate genus for this species.

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John Slapcinsky (UF) kindly gave me access to that invaluable collection. The manuscript was significantly improved by the comments of two anonymous reviewers.

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In Memoriam

William K. Emerson (1925–2016)

William K. Emerson, photo courtesy of AMNH Photographic Collection

On October 19, 2016, malacology lost one of its most respected senior members. William "Bill" Emerson died in New York City at the age of 91, following a 50-year career mainly spent at the American Museum of Natural History. It was there that he built a legacy of research, curation, and public service, including supervising world-class exhibitions and serving as President of most of this country's major malacological societies. His accolades include honorary life memberships and other tributes in recognition of his career achievements.

William Keith Emerson was born in San Diego, California, on May 1, 1925. He received a Bachelor's degree in zoology from San Diego State University in 1948, followed by a Master's in zoology from University of Southern California in 1950, and a Ph.D. in invertebrate paleontology from University of California at Berkeley in 1956.

His career at the American Museum of Natural History began in 1955, when he became Collection Manager of Quaternary Invertebrates and Assistant Curator. He was promoted to full Curator in 1966, and served as Chair of the Department of Living Invertebrates from 1960 to 1974. During his time at the Museum, he studied marine gastropods and scaphopods from the Pacific region, with a focus on systematics and biogeography. The malacology collection expanded from 74,000 to 275,000 cataloged lots, in which he was assisted by two exceptional collection managers—William E. Old, Jr. (at AMNH 1960–1982), and Walter E. Sage III (1983–1995)—well-respected experts in their own right. Although Bill often professed that he delegated all shell club interactions to his collections managers, he frequently added to their activities personally. For example, his publications list shows how often he wrote for the *New York Shell Club News*; based on their writings about Bill, he was clearly revered by its members.

Early in his career, Bill participated in extensive expeditionary work in the Pacific, focusing on molluscan communities on Pacific Islands that experienced atomic bomb testing in the early 1950s, such as Bikini Atoll. In 1957, he led the Puritan-American Museum of Natural History Expedition to western Mexico. The *Puritan* expedition produced approximately 5,000 lots of mollusks for the AMNH collection, and resulted in 20 published expedition reports in *American Museum Novitates*. Harry Lee, well-known avocational malacologist from the Jacksonville Shell Club, assisted in curating the material while a medical school freshman in New York in 1962. "I was set to work on the shells taken on the Puritan-American Expedition (western Mexico), but I'm not sure I did justice to the task as there were recurrent distractions such as conchological conversations with the Bills (Old), various other visitors, e.g., Nick Katsaras (weekly from NJ), Arieh Hadar (Israel), post-doctoral fellow Henry Coomans (Netherlands), and Tucker Abbott, now all likewise free of this mortal coil. The sessions very often continued into the tearoom of the Excelsior Hotel, across the street from the northern rampart of the AMNH, after which we'd all go our separate ways" (H. G. Lee, in litt., 27 October 2016).

Among Bill's accomplishments at AMNH was his documentation of Indo-Pacific mollusks on the eastern side of the Pacific Ocean. He reasoned that the larvae of these animals must have dispersed across deep-water barriers during anomalous warm periods, now known as El Niño events. Bill also investigated the effects of oceanic upwelling of cold water on local molluscan populations living along the western coast of North America. Using these insights about modern biogeography, he elucidated the distribution of Pleistocene molluscan communities. He was author or co-author of more than

150 research papers on molluscan taxonomy and biogeography (mainly on neogastropods and scaphopods), and of seven books, notably the popular *The American Museum of Natural History Guide to Shells: Land, Freshwater, and Marine from Nova Scotia to Florida* (Alfred A. Knopf, 1976), co-authored with Morris "Karl" Jacobson, a local shell enthusiast.

Bill was an active participant in the creation of quality exhibitions at AMNH during his career. Most notably, Bill was Chairman of the Planning Committee for "Mollusks and Mankind" (later "Mollusks and Our World," on display 1975–2000). This exhibit combined natural history, anthropology, and art, explaining the habitat and life histories of mollusks as well as their use by various cultures.

Bill served malacology as President of the Council of Systematic Malacologists (1988–1991); President of the American Malacological Union (1961–1962); President of the Western Society of Malacologists (WSM; 1968–1969); Council member of the Society of Systematic Zoology (1960–1963; 1970–1972); Trustee of the Delaware Museum of Natural History (1989–1993), and on many editorial boards. He held research associate positions at the San Diego Society of Natural History (1962–1980) and Santa Barbara Museum of Natural History (1991–2016). Although he spent his career on the East Coast, his West Coast roots ran deep; "Bill was part of the "WSM family," a treasured member of the malacologists who met annually, supported and nurtured students and others" (J. Terry Smith, in litt., 31 October 2016).

As President of the American Malacological Union (now Society), Bill organized its 28th annual meeting in 1962 in St. Petersburg, Florida, assisted by the St. Petersburg Shell Club. Resurrecting his paleontological roots, the logo of the meeting included the Florida Pleistocene gastropod *Hystrivasum horridum* (Heilprin, 1886).

Bill's many career honors include: Western Society of Malacologists Award (1972); American Malacological Union, Honorary Life Member (1987); California Academy of Sciences, Honorary Fellow (1987); and Western Society of Malacologists, Honorary Life Member (1994).

Bill retired in 1995 as Curator Emeritus in the Department of Invertebrates (later Division of Invertebrate Zoology) after more than 40 years of service. Following retirement, Bill continued to visit the Museum daily, to lunch with colleagues, keep up with the literature, and answer correspondence. He was an avid fan of the New York Yankees professional baseball team, and could frequently be seen sporting a Yankees baseball cap. Bill lost his life partner, Warren Osterwald, in 1995. He is survived by his brother James Emerson of Colorado and his nephew Jeffrey Emerson from New York City.

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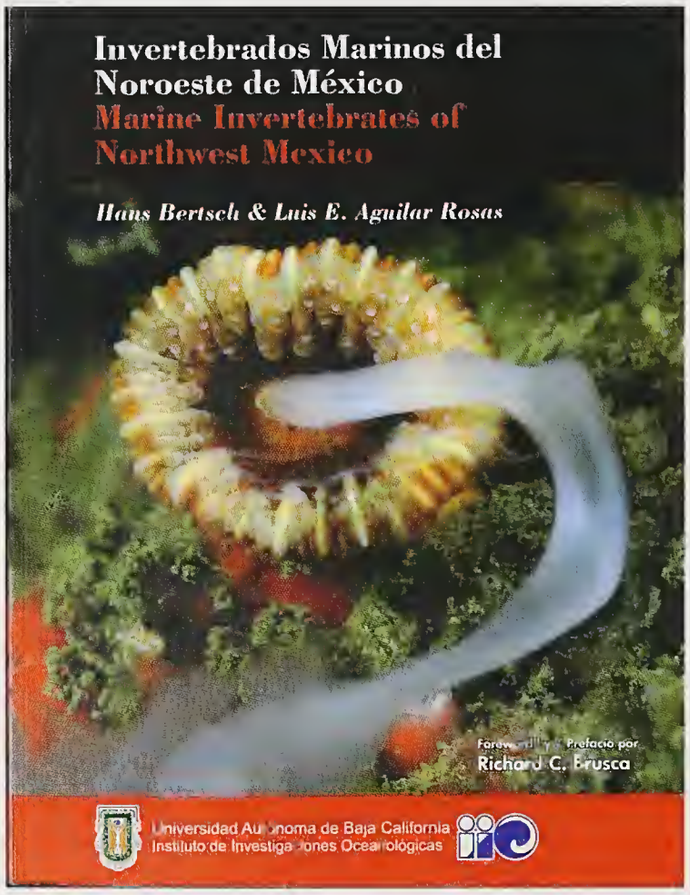
Book Review

Hans Bertsch and Luis E. Aguilar Rosas. 2016. **Invertebrados Marinos del Noroeste del México – Marine Invertebrates of Northwest Mexico.** Universidad Autónoma de Baja California, Instituto de Invetigaciones Oceanológicas, Ensenada, Mexico, 432 pp. ISBN 978-0-692-76682-8, $75 (Contact: hansmarvida@sbcglobal.net) [In English and Spanish.]

Given my lack of familiarity with the region covered in this bilingual book, I hesitated for a couple of heartbeats before accepting to review it. However, I was genuinely curious and thrilled by the concept of an international cooperation of this type, particularly one involving the invertebrate fauna of Baja California, the Gulf of California, and neighboring areas. The senior author, Hans Bertsch, is a well-known marine biologist and sea-slug specialist from southern California who has also published on some of the cultural aspects of mollusks from the region. Luis Aguilar Rosas is a respected marine biologist from the Universidad Autónoma de Baja California in Ensenada.



Knowing previous productions by the authors, I knew what to expect in terms of choice of subjects and accuracy in their reporting. However, an aspect in particular stood out during my initial examination of the book, one that expands the scope of the work into a different realm, beyond that of a traditional identification guide. The authors' unique arrangement includes precious cultural information within the treatment of many species, and in particular of mollusks. This is not at the expense of accurate and relevant taxonomic information. The biological and identification value of the book is augmented by addition of data on traditional customs of local people, including uses of some species as food, their spiritual importance, medicinal and pharmaceutical values, and others. In many cases, there is also information on the local nomenclature and the indigenous take on the folk taxonomy of those species. A typical species entry contains (in addition to the scientific and common names and great color illustrations) the subsections *Description*, *Size*, *Habitat*, [geographic] *Distribution*, and *Remarks* (cultural and ethnographic information, when available, is included in this latter subsection). Entries in the section on mollusks, in most cases, include an image of the live animal. The section on Mollusks comprises 390 species, for a total of 806 species (48 %) treated in the book (hence the relevance of this review in *The Nautilus*). There is a glossary and separate literature sections for the different groups (the literature section for Mollusca alone spans 7.5 pages). The volume also includes essays by José Luis Carballo, Donald Potts, Jesús Angel de Léon-Gonzalez, Paul Valentich-Scott, and Francisco A. Solís-Marín. The individual sections benefitted from the taxonomic expertise and contributions of a large cadre of international specialists in the different phyla. Spot checks reveal that the taxonomy and binominal nomenclature is up to the most recent standards compiled in the World Register of Marine Species (WoRMS Editorial Board, 2016.)

Did the authors aim to provide a complete guide of regional marine invertebrates for northwestern Mexico? They didn't, but this doesn't detract from the usefulness of their production. For instance, from the standpoint of mollusks, there are gaps in the taxonomic coverage of the phylum, with lack of a more comprehensive coverage for some families of microgastropods and small bivalves. It is not a purpose of the book, however, to include the entire representation of invertebrates for the covered area, but to present a selection of the most conspicuous and relevant taxa that fit in a handy book format.

This production by Bertsch and Aguilar Rosas is symbolic of a much-desired type of cooperation between

the two great North American nations. No dividing wall separates the complementary interests and important contributions from these two authors. On the contrary, there is a clear synergistic component in their work. Beyond its efficacy as an invertebrate field guide, Bertsch and Aguilar Rosas's stimulating volume transcends its regional-guide aspect to become a very readable narrative of the taxonomy, natural history, ecology, and cultural aspects of the species it covers.

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THE NAUTILUS

Volume 130
2016

AUTHOR INDEX

Amano, K. 116, 158
Amaral, V.S. 53
Bhave, V. 72
Brante, A. 153
Breure, A.S.H. 27
Bruning, P. 153
Cabrera, F. 5
Cárdenas, L. 153
Coan, E.V. 17
Combosch, D. 137
DeVries, T.J. 101
Dumale, D. 137
Fields, A. 27
García, E.F. 79, 127
Giribet, G. 137
Goddard, J.H.R. 146
Hickman, C.S. 83
Hoover, C. 146
Hovestadt, A. 27
Jenkins, R.G. 116
Kabat, A.R. 17
Landman, N.H. 166
Leal, J.H. 168
Lemer, S. 137
Lyons, W.G. 127, 134
Manríquez, P.H. 153
Martínez, S. 5
Medrano, S. 72
Mikkelsen, P.M. 166
Morales, K. 153
Norbis, W. 5
Oleinik, A.O. 116, 158
Portell, R.W. 13
Robinson, D.G. 27
Sánchez, R. 153
Schmelz, G.W. 13
Simone, L.R.L. 53
Snyder, M.A. 122, 127, 134
Soliman, V. 137
Sotto, F. 137
Valdés, Á. 72
Vermeij, G.J. 122
Watters, G.T. 23, 164
Wicksten, M.K. 132
Zhang, J. 1
Zhang, Sh. 1
Zhang, Su. 1

NEW TAXA PROPOSED IN VOLUME 130

GASTROPODA

Admete katsurihaensis Amano and Oleinik, 2016, new species (Cancellariidae, fossil) 117
Bathyacmaea lactea Zhang, Zhang, and Zhang, 2016, new species (Pectinodontidae) 3
Bathyancistrolepis mikasaensis Amano and Oleinik, 2016, new species (Buccinidae, fossil) 160
Calliotropis andamanensis Hickman, 2016, new species (Calliotropidae) 88
Calliotropis enantioserrata Hickman, 2016, new species (Calliotropidae) 86
Calliotropis locolocoensis Hickman, 2016, new species (Calliotropidae) 93
Calliotropis lumuluensis Hickman, 2016, new species (Calliotropidae) 94
Calliotropis tabakaensis Hickman, 2016, new species (Calliotropidae) 92
Calliotropis tominiensis Hickman, 2016, new species (Calliotropidae) 90
Chondropoma bellavittatum Watters, 2016, new species (Annulariidae) 23
Cuthona luciae Valdés, Medrano, and Bhave, 2016 new species (Tergipedidae) 74
Fasciolaria delicatissima García, Lyons, and Snyder, 2016, new species (Fasciolariidae) 128
Hesperaptyxis Snyder and Vermeij, 2016, new genus (Fasciolariidae) 122
Hesperaptyxis negusi Snyder and Vermeij, 2016 (Fasciolariidae) 124
Misifulgur DeVries, 2016, new genus (Buccinidae, fossil) 103
Misifulgur dockeryi DeVries, 2016, new genus (Buccinidae, fossil) 104
Misifulgur macneili DeVries, 2016, new genus (Buccinidae, fossil) 106
Misifulgur montemarensis DeVries, 2016, new genus (Buccinidae, fossil) 111
Parachondria joyeuse Watters, 2016, new species (Annulariidae) 164
Truncatella andymurrayi Schmelz and Portell, 2016, new species (Truncatellidae, fossil) 14
Truncatella chipolana Schmelz and Portell, 2016, new species (Truncatellidae, fossil) 14
Truncatella sarasotaensis Schmelz and Portell, 2016, new species (Truncatellidae, fossil) 15

REVIEWERS FOR VOLUME 130

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THE NAUTILUS publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of interest to the malacological community will appear in a notices section.

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Voucher Specimens: Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly encouraged, as is the deposition of representative voucher specimens for all other types of research work.

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